Zootaxa 3592: 1–85 (2012)
www.mapress.com/zootaxa/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

urn:lsid:zoobank.org:pub:A2D9C9ED-C0BA-4B5F-A330-C9AB7D625704

ZOOTAXA

3592

The ant genus *Tetramorium* Mayr (Hymenoptera: Formicidae) in the Malagasy region—taxonomic revision of the *T. kelleri* and *T. tortuosum* species groups

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Magnolia Press
Auckland, New Zealand

Accepted by J. Longino: 19 Nov. 2012; published: 19 Dec. 2012

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The ant genus *Tetramorium* Mayr (Hymenoptera: Formicidae) in the Malagasy region—taxonomic revision of the *T. kelleri* and *T. tortuosum* species groups

(*Zootaxa* 3592)

85 pp.; 30 cm.

19 Dec. 2012

ISBN 978-1-77557-072-1 (paperback)

ISBN 978-1-77557-073-8 (Online edition)

FIRST PUBLISHED IN 2012 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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Abstract

The taxonomy of the *T. kelleri* and *T. tortuosum* groups is revised for the Malagasy zoogeographical region. Twenty-four species are recognised of which 18 are described as new and six re-described. This raises the species richness for the genus *Tetramorium* in the Malagasy region to 84 species. The *T. kelleri* group is endemic to the Malagasy region, and contains the two species *T. ankarana* sp. n. and *T. kelleri* Forel. The *T. tortuosum* group is distributed in most zoogeographical regions, but reaches its highest species richness in the Malagasy region with the 22 species treated herein. All species are endemic to the island of Madagascar. Based on morphological key characters, the group was divided into four species complexes. The largest species complex is the *T. andrei* complex with the nine species: *Tetramorium ala* sp. n., *Tetramorium andohahela* sp. n., *Tetramorium andrei* Forel, *Tetramorium electrum* Bolton, *Tetramorium elf* sp. n., *Tetramorium isectum* Bolton, *Tetramorium isoelectrum* sp. n., *Tetramorium nify* sp. n., and *Tetramorium voasary* sp. n. The name *Tetramorium robustior* Forel is proposed as junior synonym of *T. andrei*. The most species-poor is the *T. jedi* species complex with just the three species *Tetramorium avaratra* sp. n., *Tetramorium jedi* sp. n., and *Tetramorium pleganon* Bolton. The *T. noeli* species complex holds four species: *Tetramorium aherni* sp. n., *Tetramorium ambanizana* sp. n., *Tetramorium noeli* sp. n., and *Tetramorium singletonae* sp. n. The *T. smaug* species complex includes the six species: *Tetramorium adamsi* sp. n., *Tetramorium marojejy* sp. n., *Tetramorium latreillei* Forel, *Tetramorium nazgul* sp. n., *Tetramorium sabatra* sp. n., and *Tetramorium smaug* sp. n. Furthermore, lectotypes and paralectotypes are designated

for *T. andrei* and *T. latreillei*. Both species groups are fully revised with illustrated identification keys to species level. All descriptions/re-descriptions are illustrated with high-quality multifocused montage images, and distribution maps are provided for all treated species. In addition, the taxonomic validity, species composition, and biogeography of the entire *T. tortuosum* species group is discussed on a global basis.

Key words: Madagascar, Malagasy region, taxonomy, Tetramoriini, *Tetramorium*

Introduction

The ant genus *Tetramorium* Mayr, 1855 is one of the most species-rich for ants and contains about 465 described species (Bolton, 2012). Within the Tetramoriini it is undoubtedly the largest genus, holding more than 95 % of all species within the tribe (Bolton, 1976, 2012). Though the genus is distributed throughout most zoogeographical regions, its species richness varies greatly from region to region. Around 230 species are found in the Afrotropical region (Bolton, 1976, 1980, 1985; Hita Garcia *et al*. 2010a, 2010b, 2010c). By contrast, the lowest number of species is found in the New World, which has just 16 species of *Tetramorium* (Brown, 1957, 1964; Bolton, 1977; Steiner *et al*., 2006; Vásquez-Bolaños, 2007; Marques *et al*., 2011; Vásquez-Bolaños *et al*., 2011), more than half introduced from other regions. The Palaearctic, Malagasy, Oriental, and Indo-Australian regions each harbor many more species than the New World, but significantly less than the Afrotropical region (Bolton, 1976, 1977, 1979, 1980).

The taxonomic foundation has been sound since Bolton (1976, 1977, 1979, 1980, 1985) revised the faunas of most regions, with the exception of the Palaearctic. The taxonomy of the latter region, despite never being fully revised, was improved during the last decade both at the species complex level (Csösz *et al*., 2007; Csösz & Schulz, 2010) and on the basis of integrated taxonomy approaches (Steiner *et al*., 2005; Schlick-Steiner *et al*., 2006; Steiner *et al*., 2010). The Malagasy *Tetramorium* were initially revised by Bolton (1979), who treated 36 species (29 endemics) from eight species groups. The synonymisation of the genus *Triglyphothrix* Forel under *Tetramorium* by Bolton (1985) added the tramp species *T. lanuginosum* Mayr and the *T. obesum* species group to the Malagasy *Tetramorium* fauna. In the last decade, two more tramp species from the *T. bicarinatum* group (*T. insolens* and *T. pacificum*) were reported from Mauritius and Reunion (Blard *et al*., 2003; Roberts & McGlynn, 2004). With all the above studies in mind, the Malagasy *Tetramorium* fauna consisted of 39 species from nine species groups until 2011.

Recently, Hita Garcia & Fisher (2011) began an updated taxonomic revision of the genus for the Malagasy region, and proposed and defined 14 species groups as a foundation for a large-scale revision of over 100 species on the basis of over 30,000 specimens generated by the Malagasy ant inventory project (Fisher, 2005). Together with the species group definitions, they also presented a first illustrated species group key for the Malagasy region, and revised the taxonomy of the *T. bicarinatum*, *T. obesum*, *T. sericeiventre*, and *T. tosii* groups. This work did not change the total species count of 39 due to one synonymisation and one newly described species. Recently, Hita Garcia & Fisher (2012) revised the taxonomy of the *T. bessonii*, *T. bonibony*, *T. dysalum*, *T. marginatum*, *T. tsingy*, and *T. weitzeckeri* species groups. The latter study treats 34 species, of which 27 are described as new, which raises the species count for the Malagasy region to 67. A few additional species groups also are proposed, leading to a total of 19 for the region.

Based on the above-mentioned studies, we now revise the taxonomy of the *T. kelleri* and *T. tortuosum* species groups for the Malagasy zoogeographical region. Both groups are fully revised with descriptions of 18 new species and re-descriptions of 6 formerly described species, which increases the species richness for the genus *Tetramorium* in the Malagasy region to 84 species. The descriptions are supplemented with high-quality, multifocused montage images, and illustrated identification keys are provided for both species groups. Furthermore, we discuss the taxonomic validity, species composition, and biogeography of the entire *T. tortuosum* group on a global basis.

Abbreviations of depositories

The collection abbreviations follow Bolton (1980) and Evenhuis (2009). The material upon which this study is based is located and/or was examined at the following institutions:

BMNH	The Natural History Museum (British Museum, Natural History), London, U.K.
CASC	California Academy of Sciences, San Francisco, California, U.S.A.

MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MHNG	Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland
NHMB	Naturhistorisches Museum, Basel, Switzerland
USNM	United States National Museum of Natural History, Washington, D.C., U.S.A.

Material and methods

The material examined in this study is based on ant inventories carried out in the Malagasy region from 1992 to 2012 which included more than 6,000 leaf litter samples, 4,000 pitfall traps, and 9,000 additional hand collecting events (see Fisher, 2005 for additional details).

All new type material and all imaged specimens can be uniquely identified with specimen-level codes affixed to each pin (e.g. CASENT0078328). In the presented descriptions we list all of the available specimen-level codes for the whole type series. It should be noted, however, that the number of stated paratype workers does not necessarily match the number of listed specimen-level codes because several pins hold more than one specimen. Digital colour images were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage software (version 5.0), or a Leica DFC 425 camera in combination with the Leica Application Suite software (version 3.8). All images presented are available online and can be seen on AntWeb (http://www.antweb.org). The measurements were taken with a Leica MZ 12.5 equipped with an orthogonal pair of micrometers at a magnification of 100x, rarely 80x. Measurements and indices are presented as minimum and maximum values with arithmetic means in parentheses. In addition, all measurements are expressed in mm to two decimal places. The measurements and indices used in this study are the same as in Hita Garcia and Fisher (2011, 2012):

Head length (HL):	maximum distance from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin of head, measured in full-face view. Impressions on anterior clypeal margin and posterior head margin reduce head length.
Head width (HW):	width of head directly behind the eyes measured in full-face view.
Scape length (SL):	maximum scape length excluding basal condyle and neck.
Eye length (EL):	maximum diameter of compound eye measured in oblique lateral view.
Pronotal width (PW):	maximum width of pronotum measured in dorsal view.
Weber's length (WL):	diagonal length of mesosoma in lateral view from the postero-ventral margin of propodeal lobe to the anterior-most point of pronotal slope, excluding the neck.
Propodeal spine length (PSL):	the tip of the measured spine, its base, and the centre of the propodeal concavity between the spines must all be in focus. Using a dual-axis micrometer the spine length is measured from the tip of the spine to a virtual point at its base where the spine axis meets orthogonally with a line leading to the median point of the concavity.
Petiolar node height (PTH):	maximum height of petiolar node measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node.
Petiolar node length (PTL):	maximum length of the dorsal face of the petiolar node from the anterodorsal to the posterodorsal angle, measured in dorsal view excluding the peduncle.
Petiolar node width (PTW):	maximum width of dorsal face of petiolar node measured in dorsal view.
Postpetiole height (PPH):	maximum height of the postpetiole measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node.
Postpetiole length (PPL):	maximum length of postpetiole measured in dorsal view.
Postpetiole width (PPW):	maximum width of postpetiole measured in dorsal view.

Ocular index (OI):	EL / HW * 100
Cephalic index(CI):	HW / HL * 100
Scape index (SI):	SL / HW * 100

Propodeal spine index (PSLI): PSL / HL * 100
Petiolar node index (PeNI): PTW / PW * 100
Lateral petiole index (LPeI): PTL / PTH * 100
Dorsal petiole index (DPeI): PTW / PTL * 100
Postpetiolar node index (PpNI): PPW / PW * 100
Lateral postpetiole index (LPpI): PPL / PPH * 100
Dorsal postpetiole index (DPpI): PPW / PPL * 100
Postpetiole index (PPI): PPW / PTW * 100

Note that the petiole and postpetiole were measured differently. For the petiole, only the petiolar node was measured, excluding the peduncle, as the node has proved to be of high diagnostic value (Hita Garcia *et al*., 2010c). Measurements of the whole petiole, peduncle plus node, would mask important differences between species. In contrast, we measured the whole postpetiole because it was rounded in most species and without a distinct peduncle-like structure. As a consequence, some information can be lost in the few species with a moderately or strongly anteroposteriorly compressed postpetiole. Even so, the postpetiole measurements as defined still permit better comparisons for most species.

Pubescence and pilosity are often of high diagnostic value within the genus *Tetramorium* (Bolton, 1976, 1977, 1979, 1980, 1985; Hita Garcia *et al*., 2010c, Hita Garcia & Fisher, 2011, 2012). The varying degree of inclination of pilosity is particularly important for the diagnosis of groups or species. In this context we use the terms "erect", "suberect", "subdecumbent", "decumbent", and "appressed" following Wilson (1955).

Synopsis of species of the Malagasy region examined in this study

***Tetramorium kelleri* species group**
Tetramorium ankarana **sp. n.**
Tetramorium kelleri Forel, 1887

***Tetramorium tortuosum* species group**
***Tetramorium andrei* species complex**
Tetramorium ala **sp. n.**
Tetramorium andohahela **sp. n.**
Tetramorium andrei Forel, 1892a
= *Tetramorium robustior* Forel, 1892b **syn. n.**
Tetramorium electrum Bolton, 1979
Tetramorium elf **sp. n.**
Tetramorium isectum Bolton, 1979
Tetramorium isoelectrum **sp. n.**
Tetramorium nify **sp. n.**
Tetramorium voasary **sp. n.**

***Tetramorium jedi* species complex**
Tetramorium avaratra **sp. n.**
Tetramorium jedi **sp. n.**
Tetramorium pleganon Bolton, 1979

***Tetramorium noeli* species complex**
Tetramorium aherni **sp. n.**
Tetramorium ambanizana **sp. n.**
Tetramorium noeli **sp. n.**
Tetramorium singletonae **sp. n.**

***Tetramorium smaug* species complex**
Tetramorium adamsi **sp. n.**
Tetramorium marojejy **sp. n.**
Tetramorium latreillei Forel, 1895
Tetramorium nazgul **sp. n.**
Tetramorium sabatra **sp. n.**
Tetramorium smaug **sp. n.**

Notes on the species groups treated in this study

The *T. tortuosum* group is widely distributed in the New and Old World with its main diversity centred in the Malagasy, Oriental and Indo-Australian regions. The *T. tortuosum* group fauna of the latter two regions was revised by Bolton (1977) who recognised seven Oriental and nine Indo-Australian species. Later, Sheela and Narendran (1998) described one additional species for the Oriental region. The taxonomy of the Malagasy group members was first revised by Bolton (1979). He listed seven species for the region, although our current study raises this count to 22. Surprisingly, the Afrotropical region possesses just two described species, which appears low compared to the extreme diversity of the genus in this region and the species counts for the other regions. Despite the existence of several undescribed Afrotropical species located in the collections of BMNH and CASC, the species diversity of the group will surely not reach the levels of the Malagasy, Oriental and Indo-Australian regions. In strong contrast to the latter regions, the New World has a very depauperate *Tetramorium* fauna, and the *T. tortuosum* group with its seven species is the only native group known so far (Bolton, 1979; Vásquez-Bolaños, 2007; Marques *et al*., 2011; Vásquez-Bolaños *et al.*, 2011). All other *Tetramorium* species encountered in the Americas are introduced.

Nevertheless, we are not sure if all the species currently placed in the *T. tortuosum* group represent a natural group that shares common ancestry or if they are convergent lineages within the species-rich genus *Tetramorium*. The main characters that unite them are 11-segmented antennae, the spatulate sting appendage, and the approximately rectangular nodiform shape of the petiolar node. Other group characters of less diagnostic value are the comparatively large body size, an armed propodeum, sculptured mandibles, and generally sculptured waist segments. Taking into consideration the large number of species and species groups worldwide, the above-listed characters might not be sufficient to justify a natural group.

Several differences in the development of some characters might indicate an artificial grouping. New World species tend to have a more rounded mesosoma with less developed margination between dorsal and lateral mesosoma, while this character is generally well developed in the species from other regions. Based on our studies (Hita Garcia *et al*., 2010c; Hita Garcia & Fisher, 2011, 2012), it appears that the margination from lateral to dorsal mesosoma is of high analytical value for group diagnostics. Also, some species in the Oriental and Indo-Australian region have very little sculpture on the waist segments, which is usually distinct in most other group members, but this character is also highly variable within other groups. Furthermore, some species from the Indo-Australian region have fairly long antennal scapes with SI around 100, whereas the scapes of the remainder have SI typically below 90. Consequently, it is possible that the representatives from different regions belong to different groups. The evidence to support splitting the regional faunas is too sparse, however, especially without updated taxonomic revisions of the Afrotropical, Oriental, and Indo-Australian regions which could place the *T. tortuosum* group in relation to the other groups from these regions. A molecular phylogenetic and biogeographic analysis of the genus *Tetramorium* and the tribe Tetramoriini including most known species groups does not exist, but would be greatly desirable. Such comprehensive data might provide additional insights into the relationships of the current species groupings, and shed light on the monophyly of the *T. tortuosum* group.

In Hita Garcia *et al.* (2012) we noted that *T. kelleri* might deserve placement in its own species group on the basis of the sculpture on head and mesosoma, which is mainly reticulate-rugose, compared to the mainly longitudinally rugose sculpture encountered in the remainder of the *T. tortuosum* group, in combination with the petiolar node shape. In *T. kelleri* the node is club-like with a low and rounded anterodorsal margin, which contrasts with the rectangular nodiform node of most other species, in which the anterodorsal margin is always developed and generally significantly marginate. More evidence for a separation is the margination of the mesosoma, which is poorly

developed in *T. kelleri* but generally well developed in the rest of the group. Therefore, with the Malagasy species in mind, it makes sense to separate *T. kelleri* from the other *T. tortuosum* group species, which we have done in this revision. This splitting is also supported by molecular data based on mtDNA (FHG & BLF, unpublished data).

However, the group representatives from other regions must be considered before taking this step. All of the characters mentioned to justify the separation of *T. kelleri* are found in some members of the *T. tortuosum* group outside the Malagasy region. Several species from the New World and the Oriental and Indo-Australian regions have varying levels of reticulate-rugose sculpture. The shape of the petiolar node seen in *T. kelleri*, despite being specific to the Malagasy region, is very close to the node of the Southeast Asian species *T. noratum* Bolton. Also, as noted above, some New World species have a weak margination between lateral and dorsal mesosoma, though to a lesser extent than in *T. kelleri*. This indicates the characters of the latter species are not completely unusual for the group, but only for the Malagasy region. However, no other species unites this character combination.

Based on this analysis, we have decided to retain the separation of *T. kelleri* from the *T. tortuosum* group as proposed in Hita Garcia and Fisher (2012). With the monophyly of the New and Old World *T. tortuosum* group currently uncertain, we can only offer evidence for the Malagasy region, which supports the split.

Review of species

Tetramorium kelleri species group

Diagnosis

Eleven-segmented antennae; anterior clypeal margin medially impressed; frontal carinae well-developed and usually running to posterior head margin; anterior face of mesosoma weakly developed; margination between lateral and dorsal mesosoma very weakly developed, sides round smoothly onto dorsum; propodeal spines always long to extremely long, and spinose; propodeal lobes short, triangular, and blunted or acute; petiolar node clublike, anterodorsal margin situated lower and much less pronounced than posterodorsal margin, in profile approximately as long as high, in dorsal view distinctly longer than wide; postpetiole globular to subglobular; mandibles strongly sculptured; sculpture on head, mesosoma, and waist segments distinct and predominantly reticulate-rugose; gaster unsculptured, smooth, and shiny; whole body covered with numerous, very long, fine, standing hairs; sting appendage spatulate.

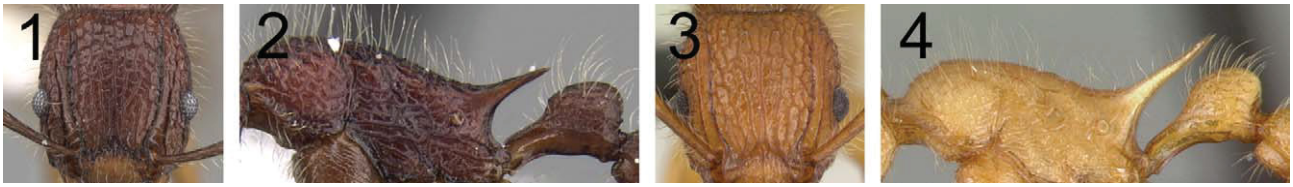
Comments

The recently (Hita Garcia & Fisher, 2012) proposed *T. kelleri* species group contains *T. kelleri* and the new species *T. ankarana*. It is mainly distributed in the north and west of Madagascar, as well as on Nosy Be and Mayotte, and both species prefer forested habitats.

Other *Tetramorium* species from a different species group are unlikely to be confused with *T. ankarana* or *T. kelleri*. The possession of 11-segmented antennae and the very conspicuous petiolar node shape clearly distinguish them from all other Malagasy species groups.

Key to species of the *T. kelleri* species group (workers)

1. Species with smaller eyes (OI 20); relatively longer antennal scapes (SI 101–104); and long propodeal spines (PSLI 35–38) (Figs. 1, 2). . . . . *T. ankarana*
- Species with larger eyes (OI 24–26); relatively shorter antennal scapes (SI 89–99); and extremely long propodeal spines (PSLI 49–68) (Figs. 3, 4). . . . . *T. kelleri*



FIGURES 1–4. 1. *T. ankarana* (CASENT0247543) head in full-face view. **2**. *T. ankarana* (CASENT0247543) mesosoma in profile. **3.** *T. kelleri* (CASENT0132658) head in full-face view. **4.** *T. kelleri* (CASENT0132658) mesosoma in profile.

***Tetramorium ankarana* Hita Garcia & Fisher sp. n.**
(Figs. 1, 2, 5, 6, 7, 141)

Holotype worker, MADAGASCAR, Antsiranana, Réserve Ankarana, 7 km SE Matsaborimanga, 12° 54' S, 49° 07' E, 150 m, rainforest, ground foragers, collection code PSW11043, 30.XI.1990 (*P.S. Ward*) (CASC: CASENT0247543). Paratypes, one worker with same data as holotype (BMNH: CASENT0247311); and two workers from Antsiranana, Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, 12.90889 S, 49.10983 E, 80 m, tropical dry forest, on low vegetation, collection code BLF03007, 10.–16.II.2001 (*B.L. Fisher, C. Griswold et al.*) (CASC: CASENT0404423; CASENT0427943).

Diagnosis
Tetramorium ankarana can be easily distinguished from *T. kelleri* by the following character combination: much smaller eyes (OI 20); relatively longer antennal scapes (SI 101–104); and long propodeal spines (PSLI 35–38).

Description
HL 0.97–1.02 (0.99); HW 0.85–0.89 (0.86); SL 0.88–0.90 (0.88); EL 0.17–0.18 (0.17); PH 0.47–0.50 (0.49); PW 0.66–0.72 (0.69); WL 1.21–1.31 (1.26); PSL 0.34–0.37 (0.36); PTL 0.33–0.36 (0.35); PTH 0.34–0.36 (0.35); PTW 0.26–0.29 (0.28); PPL 0.28–0.31 (0.29); PPH 0.34–0.37 (0.35); PPW 0.33–0.37 (0.35); CI 87–88 (87); SI 101–104 (102); OI 20 (20); DMI 54–56 (55); LMI 37–40 (39); PSLI 35–38 (36); PeNI 39–42 (41); LPeI 97–100 (99); DPeI 79–84 (81); PpNI 50–52 (51); LPpI 81–85 (83); DPpI 116–125 (120); PPI 122–128 (125) (four measured).

Head much longer than wide (CI 87–88); posterior head margin very weakly concave. Anterior clypeal margin medially impressed, often weakly so. Frontal carinae strongly developed, approaching corners of posterior head margin. Antennal scrobes well-developed, moderately deep, narrow, and without defined posterior margin; ventral margin moderately defined. Antennal scapes long, reaching posterior head margin (SI 101–104). Eyes small (OI 20). Mesosomal outline in profile flat to weakly convex, very weakly marginate from lateral to dorsal mesosoma, sides rounding smoothly onto the dorsum; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–40). Propodeal spines long, spinose and acute (PSLI 35–38); propodeal lobes short, triangular, and rounded. Petiolar node in profile clublike with fairly rounded margins, approximately as long as high (LPeI 97–100), anterodorsal margin situated lower than posterodorsal margin, dorsum noticeably convex; node in dorsal view approximately 1.2 to 1.3 times longer than wide (DPeI 79–84). Postpetiole in profile globular, approximately 1.2 times higher than long (LPpI 81–85); in dorsal view around 1.1 to 1.3 times wider than long (DPpI 116–125). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view 1.2 to 1.3 times wider than petiolar node (PPI 122–128). Mandibles strongly striate; clypeus longitudinally rugose/rugulose, with three to four rugae/rugulae, median ruga always present and distinct, remaining rugae weaker; cephalic dorsum between frontal carinae reticulate-rugose to longitudinally rugose, posteriorly more reticulate-rugose and anteriorly more longitudinally rugose; lateral and ventral head mostly reticulate-rugose. Mesosoma dorsally mainly reticulate-rugose, laterally reticulate-rugose to longitudinally rugose. Forecoxae usually with weak to moderately developed longitudinal rugae/rugulae. Waist segments mainly longitudinally rugulose, less reticulate-rugulose. First gastral tergite unsculptured, smooth, and shining. Whole body covered with numerous, very long, fine standing hairs. Body of uniform dark reddish brown colour.

Notes
The new species is currently only known from the type locality Ankarana where it was collected in tropical dry forest and rainforest at elevations of 80 to 150 m.

Tetramorium ankarana is the second species known from the species group, and it is easily distinguishable from *T. kelleri*. The latter species has much larger eyes (OI 24–26), relatively shorter antennal scapes (SI 89–99), and extremely long propodeal spines (PSLI 49–68), whereas *T. ankarana* possesses significantly smaller eyes (OI 20), slightly longer antennal scapes (SI 101–104), and much shorter propodeal spines (PSLI 35–38). Furthermore, *T. ankarana* is also much darker in colour than most of the material of *T. kelleri*, which ranges from whitish-yellowish to brown. However, some series were almost the same colour as *T. ankarana*, and we do not consider colouration a good diagnostic character in this case.

FIGURES 5–7. *T. ankarana*, holotype (CASENT0247543). **5.** Body in profile. **6.** Body in dorsal view. **7.** Head in full-face view.

Etymology
The name of the new species refers to the type locality, the Réserve Spéciale de l'Ankarana. The reserve is of high importance for the conservation of animal biodiversity, and the dedication of this new species accounts for its importance. The species epithet is a noun in apposition, and thus invariant.

Material examined
MADAGASCAR: Antsiranana, Réserve Ankarana, 7 km SE Matsaborimanga, 12° 54' S, 49° 07' E, 150 m, rainforest, 30.XI.1990 (*P.S. Ward*); Antsiranana, Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, 12.90889 S, 49.10983 E, 80 m, tropical dry forest, 10.–16.II.2001 (*B.L. Fisher, C. Griswold et al.*).

Tetramorium kelleri Forel, 1887
(Figs. 3, 4, 8, 9, 10, 141)

Tetramorium (*Xiphomyrmex*) *kelleri* Forel, 1887:385. Syntype workers, MADAGASCAR, Toamasina, Ivondro, pr. Tamatave (*C. Keller*). (BMNH: CASENT0102339; NHMB: CASENT0101138; MCZ: CASENT0247309; CASENT0247310; MHNG: CASENT0101293; CASENT0101294; CASENT0101938; USNM) [all examined, except material from USNM].

Diagnosis
Tetramorium kelleri differs from *T. ankarana* by the character combination of: large eyes (OI 24–26); relatively shorter antennal scapes (SI 89–99); and extremely long propodeal spines (PSLI 49–68).

Description
HL 0.98–1.11 (1.03); HW 0.85–0.97 (0.90); SL 0.79–0.90 (0.85); EL 0.21–0.24 (0.22); PH 0.45–0.58 (0.52); PW 0.66–0.80 (0.73); WL 1.29–1.48 (1.37); PSL 0.50–0.73 (0.59); PTL 0.36–0.44 (0.40); PTH 0.37–0.44 (0.40); PTW 0.29–0.36 (0.33); PPL 0.32–0.37 (0.34); PPH 0.38–0.44 (0.40); PPW 0.37–0.43 (0.40); CI 84–89 (87); SI 89–99 (94); OI 24–26 (25); DMI 50–59 (53); LMI 35–40 (38); PSLI 49–68 (57); PeNI 41–50 (46); LPeI 95–102 (99); DPeI 79–86 (83); PpNI 49–59 (55); LPpI 81–90 (86); DPpI 109–124 (117); PPI 114–126 (121) (25 measured).

Head much longer than wide (CI 84–89); posterior head margin very weakly concave. Anterior clypeal margin medially impressed, often weakly so. Frontal carinae strongly developed, approaching corners of posterior head margin. Antennal scrobes well-developed, moderately deep, narrow, and without defined posterior margin; ventral margin moderately defined. Antennal scapes moderately long to long, reaching posterior head margin (SI 89–99). Eyes large (OI 24–26). Mesosomal outline in profile flat to weakly convex, very weakly marginate from lateral to dorsal mesosoma, sides rounding smoothly onto the dorsum; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 35–40). Propodeal spines extremely long, spinose and acute (PSLI 49–68); propodeal lobes short, triangular, and rounded, sometimes weakly acute. Petiolar node in profile clublike with fairly rounded margins, ranging from weakly longer than high to weakly higher than long (LPeI 95–102), anterodorsal margin situated lower than posterodorsal margin, dorsum noticeably convex; node in dorsal view approximately 1.2 to 1.3 times longer than wide (DPeI 79–86). Postpetiole in profile globular to subglobular, approximately 1.1 to 1.2 times higher than long (LPpI 81–90); in dorsal view around 1.1 to 1.3 times wider than long (DPpI 109–124). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view 1.1 to 1.3 times wider than petiolar node (PPI 114–126). Mandibles strongly striate; clypeus longitudinally rugose/rugulose, median ruga always present and distinct, remaining rugae/rugulae weaker and variably developed; cephalic dorsum between frontal carinae reticulate-rugose to longitudinally rugose, posteriorly more reticulate-rugose and anteriorly more longitudinally rugose; lateral and ventral head mostly reticulate-rugose. Mesosoma dorsally mainly reticulate-rugose, laterally reticulate-rugose to longitudinally rugose. Forecoxae usually with weak to moderately developed longitudinal rugae/rugulae, sometimes reduced. Waist segments mainly longitudinally rugulose, less reticulate-rugulose. First gastral tergite unsculptured, smooth, and shining. Whole body covered with numerous, very long, fine standing hairs. Body of uniform whitish-yellowish to brown, mostly yellowish to orange-brown.

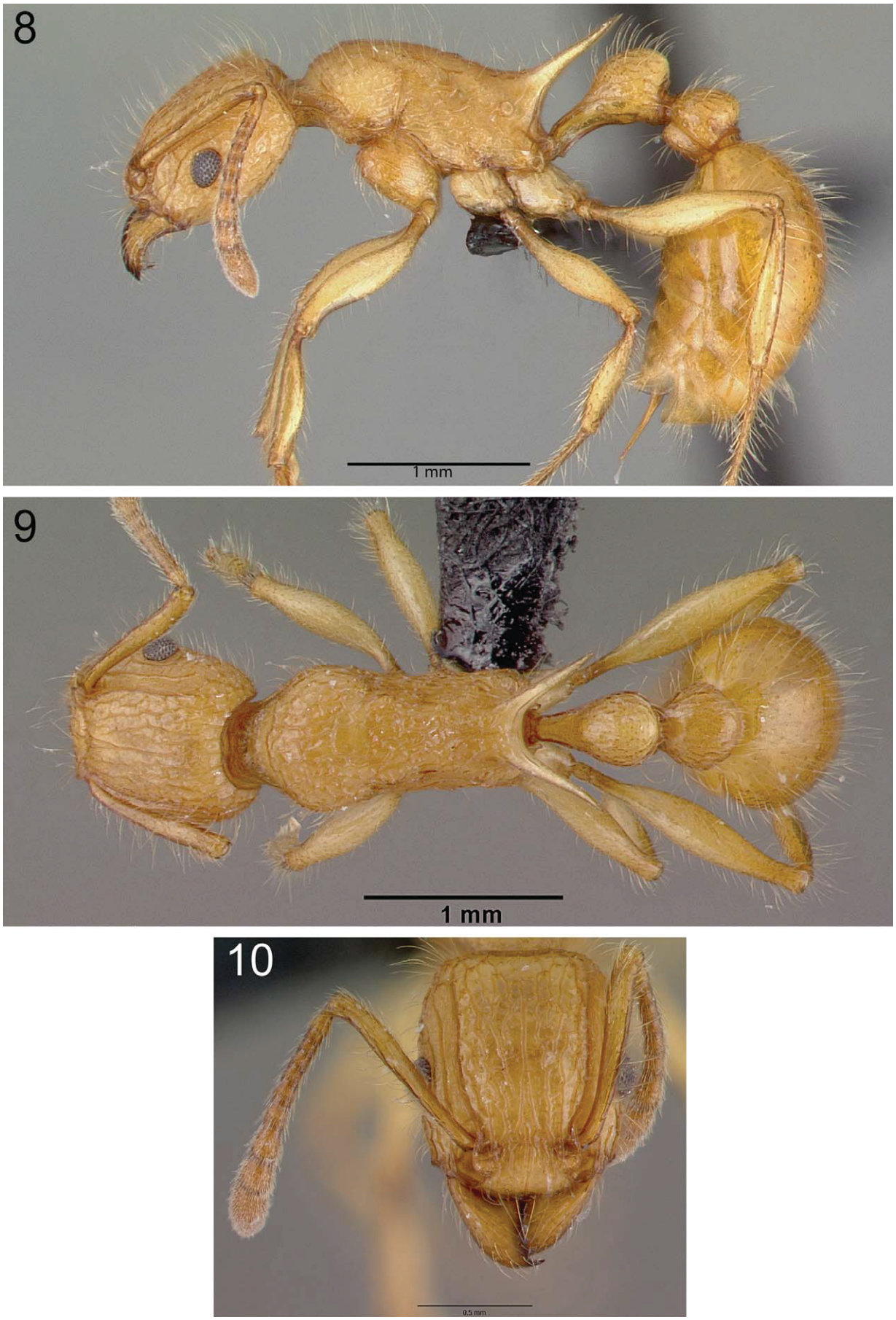
Notes
Tetramorium kelleri is mainly encountered in northern and western Madagascar, and on several islands including Nosy Be, Nosy Mangabe, and Nosy Ngontsy. Interestingly, most localities are in relatively close proximity to the

ocean since no material was collected more than 50 km inland. One aspect that deserves attention, however, is the type locality, the Ivondro River, which is relatively far from the currently known distribution range mentioned above. The area around the Ivondro River in eastern Madagascar was intensively sampled by the Malagasy ant inventory (see Fisher, 2005), but no additional *T. kelleri* material was found. Indeed, not a single modern specimen is known from eastern Madagascar south of Nosy Mangabe. One possible explanation could be that the species was present in the area over 120 years ago, but did not survive until the present day. This is surprising, though, since the species is comparatively flexible in its habitat requirements. It was collected from rainforest, littoral rainforest, tropical dry forest, and secondary forest at elevations from 5 to 780 m, although mostly at the lower range.

Despite being a very common species with a relatively broad distribution range, which includes several islands, *T. kelleri* remains remarkably invariable. Some minor variation in colouration is observed ranging from whitish-yellowish to brown, although we do not think it significant for species diagnostics. In general, as already stated by Bolton (1979), it is a highly conspicuous and easily recognisable Malagasy ant species. The only other species it could be confused with is the second species of the *T. kelleri* group, *T. ankarana*. The latter species, however, has much smaller eyes (OI 20) and propodeal spines (PSLI 35–38), and slightly longer antennal scapes (SI 101–104) than *T. kelleri* (OI 24–26; SI 89–99; PSLI 49–68).

Material examined

MADAGASCAR: Antsiranana, Ambondrobe, 41.1 km 175° Vohemar, 13.7153 S, 50.1017 E, 10 m, littoral rainforest, 30.XI.–1.XII.2004 (*B.L. Fisher*); Antsiranana, Réserve Spéciale d'Ambre, 3.5 km 235° SW Sakaramy, 12.4689 S, 49.2422 E, 325 m, tropical dry forest, 26.–31.I.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Ampahana, 18 km N Antalaha, 14° 46' S, 50° 13' E, 1 m, lowland forest, 5.II.1991 (*G.D. Alpert*); Antsiranana, Forêt d' Andavakoera, 21.4 km 75° ENE Ambilobe, 4.6 km 356° N Betsiaka, 13.1183 S, 49.23 E, 425 m, rainforest, 15.XII.2003 (*B.L. Fisher*); Antsiranana, 5 km SW Antalaha, 14° 56' 17" S, 50° 15' 42" E, 50 m, secondary forest, 10.II.1991 (*G.D. Alpert*); Antsiranana, Forêt d' Antsahabe, 11.4 km 275° W Daraina, 13.2117 S, 49.5567 E, 550 m, tropical dry forest, 12.XII.2003-16.XI.2004 (*B.L. Fisher*); Antsiranana, Forêt de Binara, 7.5 km 230° SW Daraina, 13.255 S, 49.6167 E, 375 m, tropical dry forest, 1.–2.XII.2003 (*B.L. Fisher*); Antsiranana, 6 km N Cap Est, 5 m, 20.I.1991 (*G.D. Alpert*); Antsiranana, R.S. Manongarivo, 10.8 km 229° SW Antanambao, 13.9767 S, 48.4233 E, 780 m, rainforest, 11.–17.X.1998 (*B.L. Fisher*); Antsiranana, R.S. Manongarivo, 10.8 km 229° SW Antanambao, 13.9617 S, 48.4333 E, 400 m, rainforest, 8.–13.XI.1998 (*B.L. Fisher*); Antsiranana, 2 km NE Marofinaritra, 15° 3' S, 50° 9' E, 50 m, lowland forest, 8.II.1991 (*G.D. Alpert*); Antsiranana, Nosy Be, 4 km ENE Andoany, (=Helleville), 13° 25' S, 48° 18' E, 200 m, rainforest, 2.V.1989 (*P.S. Ward*); Antsiranana, Nosy Be, Réserve Naturelle Intégrale de Lokobe, 6.3 km 112° ESE Hellville, 13.4193 S, 48.3312 E, 30 m, rainforest, 19.–24.III.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Nosy Ngontsy, 55 km S Antalaha, 15° 15' 51.9" S, 50° 29' 21.5" E, 1m, secondary rainforest, 21.I.1991 (*G.D. Alpert*); Antsiranana, Sakaramy, 12.4411 S, 49.232 E, 260 m, tropical dry forest, 11.–12.V.2011 (*B.L. Fisher et al.*); Mahajanga, Réserve Spéciale de Bemarivo, 23.8 km 223° SW Besalampy, 16.925 S, 44.3683 E, 30 m, tropical dry forest, 19.–23.XI.2002 (*B.L. Fisher, C. Griswold et al.*); Mahajanga, Parc National de Namoroka, 16.9 km 317° NW Vilanandro, 16.4067 S, 45.31 E, 100 m, tropical dry forest, 12.–16.XI.2002 (*B.L. Fisher, C. Griswold et al.*); Toamasina, Ivondro, pr. Tamatave (*C. Keller*); Toamasina, Nosy Mangabe, 7.43 km S Maroantsetra, 15.4973 S, 49.7622 E, 5 m, littoral rainforest edge, 26.VII.2007 (*B.L. Fisher et al.*); **MAYOTTE**: Mt. Benara, 12.8758 S, 45.1567 E, 425 m, 30.XI.–2.XII.2007 (*B.L. Fisher et al.*); Mt. Chongui, 12.8 S, 45.1 E, 360 m, forest near fallen tree, 15.II.–3.III.1999 (*R. Jocque & G. DeSmet*); Mt. Chongui, 12.9578 S, 45.134 E, 470 m, rainforest, 28.XI.2007 (*B.L. Fisher et al.*); Mt. Chongui, 12.959 S, 45.1341 E, 380 m, rainforest, 28.–30.XI.2007 (*B.L. Fisher et al.*); Mt. Combani, 12.8 S, 45.1333 E, 470 m, forest litter, 22.–24.II.1999 (*R. Jocque & G. DeSmet*); Mt. Combani, 12.8063 S, 45.1531 E, 370 m, rainforest, 25.XI.–4.XII.2007 (*B.L. Fisher et al.*); Mt. Combani, 12.8049 S, 45.1527 E, 460 m, rainforest, 29.XI.2007 (*B.L. Fisher et al.*); Coconi, DAF Campus, 12.8333 S, 45.1333 E, 15.I.1999 (*R. Jocque & G. DeSmet*); Dapani, 12.9628 S, 45.1504 E, 135 m, rainforest, 2.–4.XII.2007 (*B.L. Fisher et al.*); Reserve Forestiére Majimbini, 12.768 S, 45.1861 E, 525 m, rainforest, 3.XII.2007 (*B.L. Fisher et al.*); Reserve Forestiére Majimbini, 12.7689 S, 45.1902 E, 350 m, rainforest, 3.XII.2007 (*B.L. Fisher et al.*); Tsingoni, 12.7833 S, 45.1 E, litter of shrubs on mangrove edge, 27.II.–4.III.1999 (*R. Jocque & G. DeSmet*).



FIGURES 8–10. *T. kelleri* (CASENT0467063). **8.** Body in profile. **9.** Body in dorsal view. **10.** Head in full-face view.

Tetramorium tortuosum species group

Diagnosis

Eleven-segmented antennae; anterior clypeal margin medially impressed; frontal carinae well-developed and usually running to posterior head margin; anterior face of mesosoma weakly developed; margination between lateral and dorsal mesosoma generally well-developed; propodeal spines always long to extremely long, spinose, and acute (PSLI 28–72); propodeal lobes usually well-developed, triangular to elongate-triangular, generally short and acute, rarely strongly reduced to almost absent; petiolar node rectangular nodiform, anterodorsal and posterodorsal margins usually well-defined, anterior and posterior faces often parallel, node longer than wide in most species, broader than long in few species; postpetiole usually globular to subglobular; mandibles strongly sculptured in most species; head and mesosoma with distinct and predominantly longitudinally rugose sculpture; waist segments with distinctly rugose, rarely rugulose, sculpture; gaster unsculptured, smooth and shiny in many species, but sculpture present on the first gastral tergite in several species; in most species all dorsal surfaces of head, mesosoma, waist segments and gaster with abundant, long, standing hairs; sting appendage spatulate.

Comments

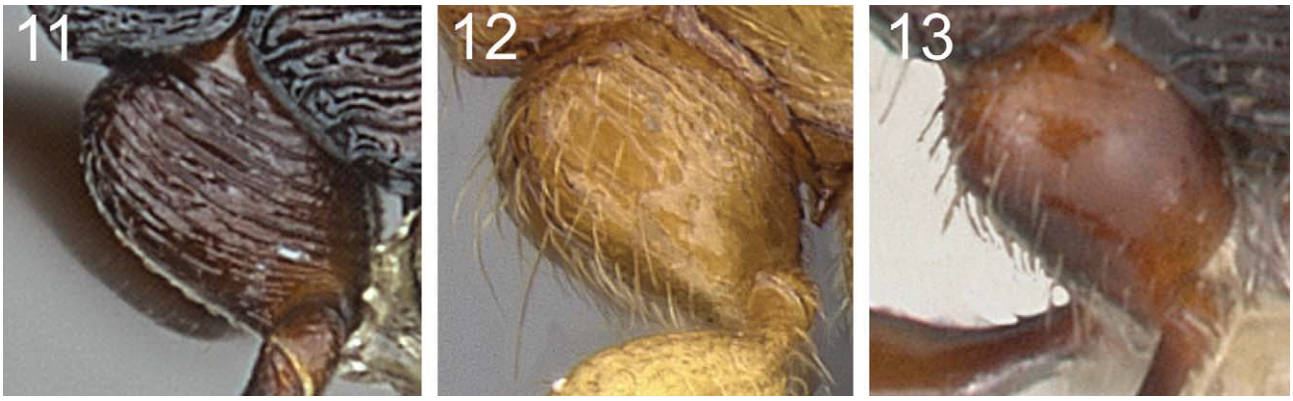
Within the Malagasy region, the *T. tortuosum* group is easily recognisable within the groups with 11-segmented antennae. The distinction from the *T. kelleri* group was explained in detail above. The *T. plesiarum* group is characterised by its distinct and conspicuous antennal scrobes with well-defined margins all-around. By contrast, the scrobes are usually developed, but less conspicuous and without well-defined posterior and ventral margins in the *T. tortuosum* group. Due to the presence of distinct sculpture on both waist segments, the group cannot be mistaken for the *T. bessonii*, *T. marginatum*, *T. naganum*, *T. schaufussii*, *T. severini*, *T. tsingy*, or *T. weitzeckeri* groups, nor parts of the *T. bonibony* and *T. dysalum* groups. The species of the *T. bonibony* group with sculptured waist segments have reticulate-rugose sculpture on the posterior head and anterior mesosoma which is not present in the *T. tortuosum* group. Most species of the *T. dysalum* group with sculptured waist segments usually have a weakly sculptured petiolar node which distinguishes them from the *T. tortuosum* group species. *Tetramorium dysalum* has more sculpture, and could be misidentified with *T. avaratra* or *T. pleganon* on the basis of petiolar node shape, but the latter species have sculptured mandibles and sculpture on the first gastral tergite, whereas *T. dysalum* possesses smooth mandibles and lacks sculpture on the first gastral tergite. Moreover, the *T. ranarum* group, despite sharing the rectangular nodiform shape of the petiolar node in some species, differs in several other important aspects, making it easily separable from the *T. tortuosum* group. The sculpture on posterior head and mesosoma is usually reticulate-rugose in the *T. ranarum* group but longitudinally rugose in the *T. tortuosum* group. Also, the propodeal spines are also much longer in the latter group than in the *T. ranarum* group. In addition, the frontal carinae and antennal scrobes are often much weaker in the *T. ranarum* group, and several species have one or even both waist segments unsculptured, whereas all Malagasy *T. tortuosum* group species have both waist segments noticeably sculptured.

Most Malagasy *T. tortuosum* group members appear to form a natural grouping except for *T. avaratra* and *T. pleganon*. In these two the petiolar node has a shape with the anterodorsal margin situated higher than the posterodorsal and the dorsum tapers distinctly backwards posteriorly, which, as mentioned above, is also seen in the *T. dysalum* group. The true affinities of *T. avaratra* and *T. pleganon* are unclear at the moment, and might be revealed by the use of molecular data in future studies. At present, however, we place them in the *T. tortuosum* group since they seem to fit best in this group until more data becomes available.

Our revision has revealed a remarkable 22 species within the *T. tortuosum* group, which makes it the most species-rich *Tetramorium* species group in the Malagasy region. In order to facilitate the work with this comparatively high number of species, we have split the group into four species complexes on the basis of few important and conspicuous morphological key characters.

Key to species of the *T. tortuosum* species group (workers)

1. In profile forecoxae completely covered with very distinct, strong, longitudinal rugae (*T. smaug* species complex) (Fig. 11) 2
- In profile forecoxae without very distinct, strong, longitudinal rugae; usually unsculptured, smooth and shining, but often with traces of rugulae or punctate sculpture (Figs. 12, 13) 9

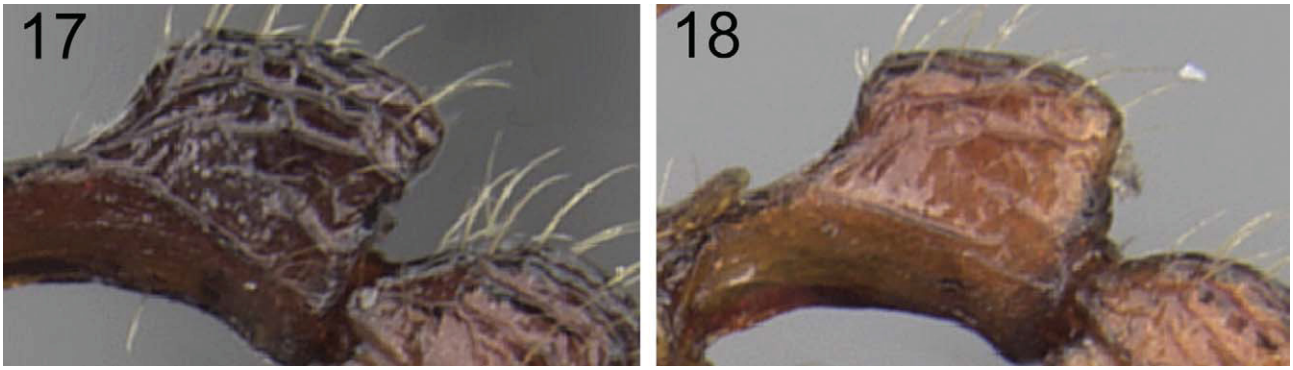


FIGURES 11–13. 11. *T. sabatra* (CASENT0189240) forecoxa in profile. **12.** *T. elf* (CASENT0045788) forecoxa in profile. **13.** *T. andrei* (CASENT0102395) forecoxa in profile.

2. Propodeal spines long to extremely long (PSLI 34–50, generally below 45); comparatively hairy species with numerous long standing hairs on the first gastral tergite (Fig. 14) 3
- Propodeal spines always extremely long (PSLI 48–72; generally above 50); less hairy species with no or few scattered, long standing hairs (Figs. 15, 16) 7

FIGURES 14–16. 14. *T. adamsi* (CASENT0247296) body in profile. **15.** *T. sabatra* (CASENT0189240) body in profile. **16.** *T. latreillei* (CASENT0101291) body in profile.

3. Petiolar node with posterodorsal margin situated higher than anterodorsal, dorsum convex (Fig. 17) . . . . . *T. adamsi*
- Petiolar node with anterodorsal and posterodorsal margins at about the same height, dorsum flat to weakly convex (Fig. 18) . . . 4

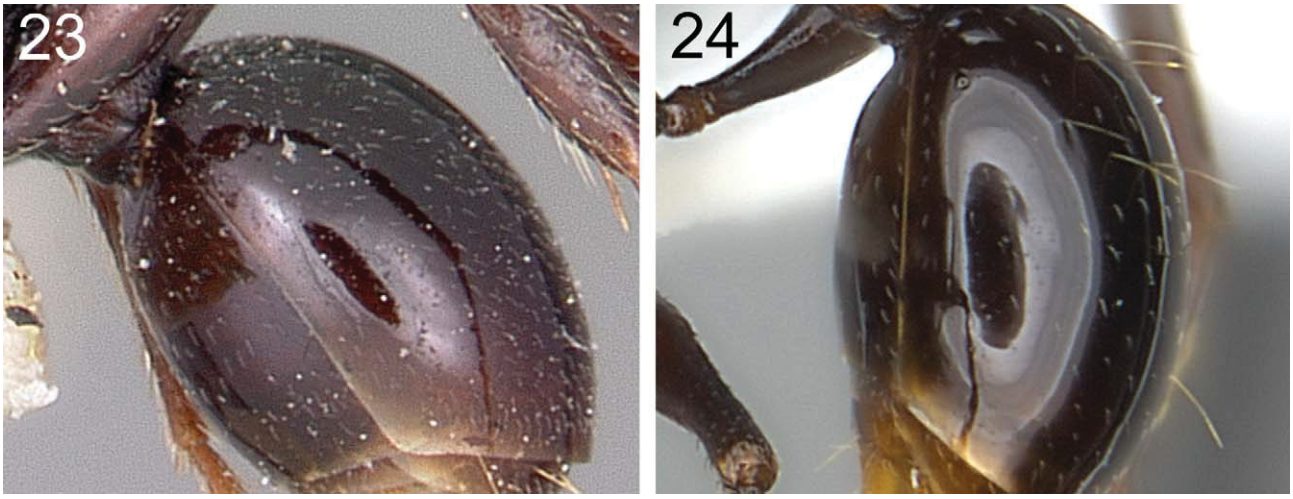


FIGURES 17 & 18. 17. *T. adamsi* (CASENT0247345) petiolar node in profile. **18.** *T. marojejy* (CASENT0247334) petiolar node in profile.

4. Antennal scapes comparatively long (SI 89–92); petiolar node higher (LPeI 81–88); body colour dark brown to black (Figs. 19, 20) . . . . . *Tetramorium nazgul*
- Antennal scapes shorter than above (SI 79–85); petiolar node lower (LPeI 89–97); body colour orange to light brown (Figs. 21, 22) . . . . . *Tetramorium marojejy*

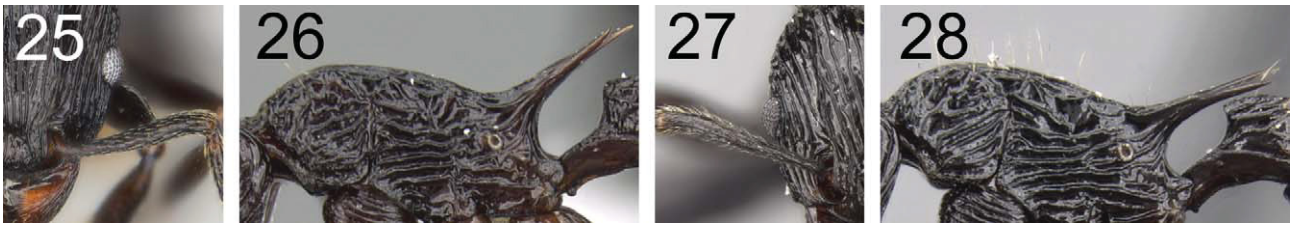
FIGURES 19–22. 19. *T. nazgul* (CASENT0028625) head in profile. **20.** *T. nazgul* (CASENT0028625) body in profile. **21.** *T. marojejy* (CASENT0247334) head in profile. **22.** *T. marojejy* (CASENT0247334) body in profile.

7. First gastral tergite without any standing hairs, only with moderately dense appressed pubescence (Fig. 23) . . . . . *Tetramorium latreillei*
- First gastral tergite with several standing hairs and scarce pubescence (Fig. 24). 8



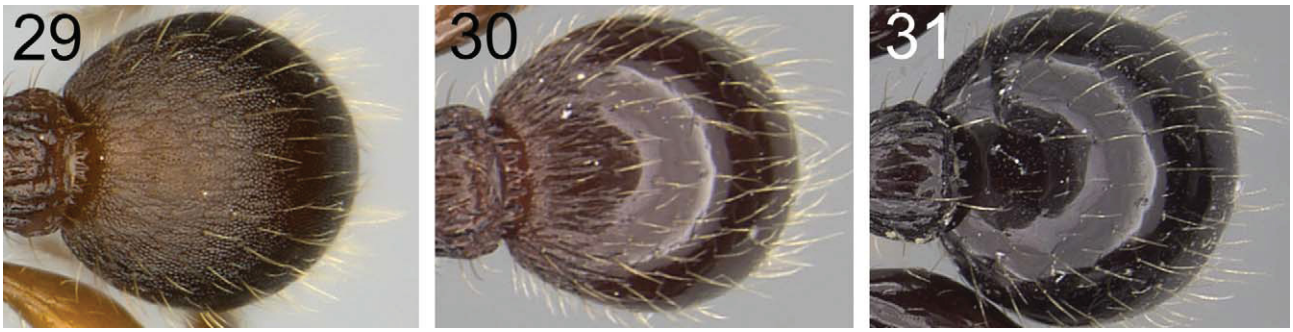
FIGURES 23 & 24. 23. *T. latreillei* (CASENT0101291) gaster in profile. **24.** *T. sabatra* (CASENT0189240) gaster in profile.

8. Leading edges of antennal scapes with appressed hairs; mesosoma with just one to two pairs of standing hairs on the pronotal dorsum (Figs. 25, 26) . . . . . *Tetramorium sabatra*
- Leading edges of antennal scapes with subdecumbent to suberect hairs; mesosoma with 7 to 14 pairs of standing hairs throughout the whole mesosomal dorsum (Figs. 27, 28). . . . . *Tetramorium smaug*



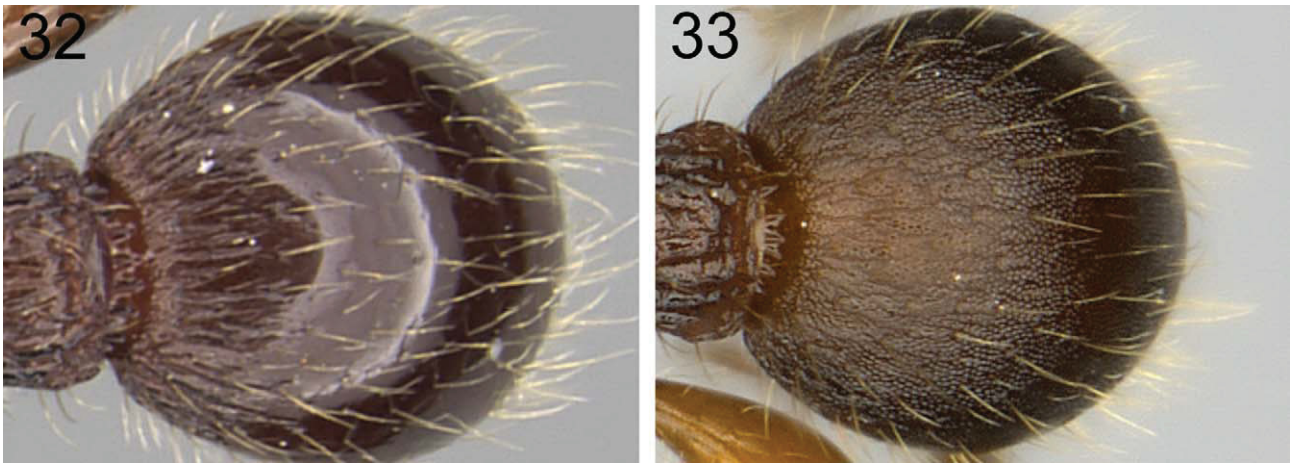
FIGURES 25–28. 25. *T. sabatra* (CASENT0048680) antennal scape in frontal view. **26.** *T. sabatra* (CASENT0189241) mesosoma in profile. **27.** *T. smaug* (CASENT0121244) antennal scape in frontal view. **28.** *T. smaug* (CASENT0121244) mesosoma in profile.

9. First gastral tergite with either reticulate-punctate or costulate sculpture (Figs. 29, 30) 10
- First gastral tergite unsculptured, smooth, and shining (*T. andrei* species complex) (Fig. 31). 16



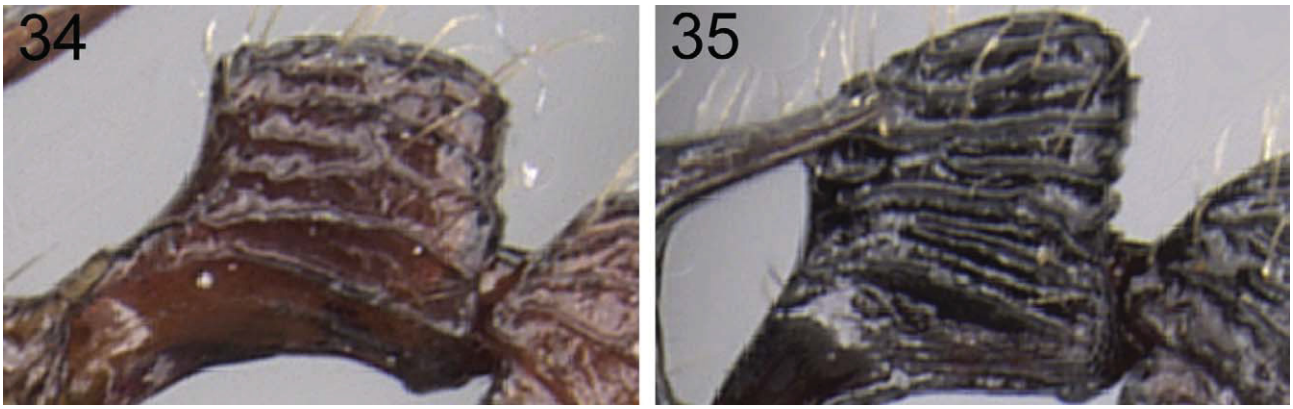
FIGURES 29–31. 29. *T. jedi* (CASENT0046064) first gastral tergite in dorsal view. **30.** *T. singletonae* (CASENT0247161) first gastral tergite in dorsal view. **31.** *T. electrum* (CASENT0280850) first gastral tergite in dorsal view.

10. First gastral tergite with basigastral costulae (*T. noeli* species complex) (Fig. 32). 11
- First gastral tergite differently sculptured (*T. jedi* species complex) (Fig. 33) 14



FIGURES 32 & 33. 32. *T. singletonae* (CASENT0247161) first gastral tergite in dorsal view. **33.** *T. jedi* (CASENT0046064) first gastral tergite in dorsal view.

11. In profile view, petiolar node with anterodorsal and posterodorsal margins at about the same height, and the dorsum flat to weakly convex (Fig. 34) 12
- In profile view, petiolar node with the posterodorsal margin situated higher than the anterodorsal margin, and the dorsum convex (Fig. 35) 13

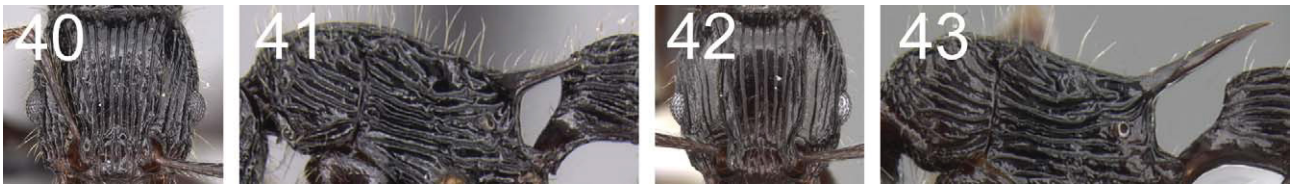


FIGURES 34 & 35. 34. *T. aherni* (CASENT0045755) petiolar node in profile. **35.** *T. noeli* (CASENT0043554) petiolar node in profile.

12. Eyes comparatively moderate to large (OI 22–24); propodeal spines comparatively long (PSLI 41–45) (Figs. 36, 37). . . . . *Tetramorium aherni*
- Eyes comparatively small (OI 16–17); propodeal spines comparatively short (PSLI 27–29) (Figs. 38, 39) . . . . . *Tetramorium singletonae*

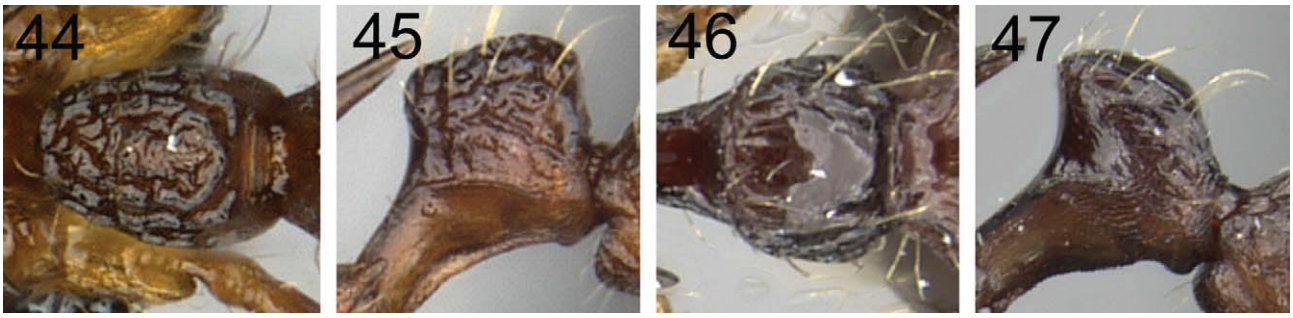
FIGURES 36–39. 36. *T. aherni* (CASENT0045755) head in full-face view. **37.** *T. aherni* (CASENT0045755) mesosoma in profile. **38.** *T. singletonae* (CASENT0247161) head in full-face view. **39.** *T. singletonae* (CASENT0247161) mesosoma in profile.

13. Head distinctly longer than wide (CI 92–95); propodeal spines extremely long but comparatively shorter than below (PSLI 38–48); postpetiole relatively higher (LPpI 68–72) and broader (DPpI 119–129) (Figs. 40, 41) . . . . . *Tetramorium noeli*
- Head weakly longer than wide (CI 97–98); propodeal spines extremely long but comparatively longer than above (PSLI 60–65); postpetiole relatively lower (LPpI 77–81) and narrower (DPpI 104–112) (Figs. 42, 43). . . . *Tetramorium ambanizana*



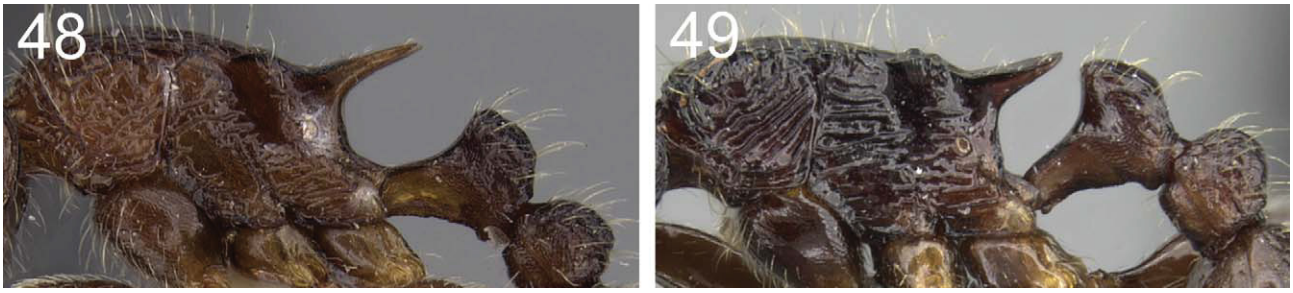
FIGURES 40–43. 40. *T. noeli* (CASENT0043554) head in full-face view. **41.** *T. noeli* (CASENT0043554) mesosoma in profile. **42.** *T. ambanizana* (CASENT0189238) head in full-face view. **43.** *T. ambanizana* (CASENT0189238) mesosoma in profile.

14. Petiolar node in dorsal view distinctly longer than wide (DPeI 79–85), in profile anterodorsal and posterodorsal margins at about same height; first gastral tergite completely covered with distinct reticulate-punctate sculpture (Figs. 44, 45) . . . . *T. jedi*
- Petiolar node in dorsal view distinctly wider than long (DPeI 111–137); in profile anterodorsal margin situated higher than posterodorsal margin and dorsum tapering backwards; first gastral tergite never completely covered with distinct reticulate-punctate sculpture, generally with superficial reticulate-punctate sculpture restricted to the basal first half of the tergite (Figs. 46, 47) 15



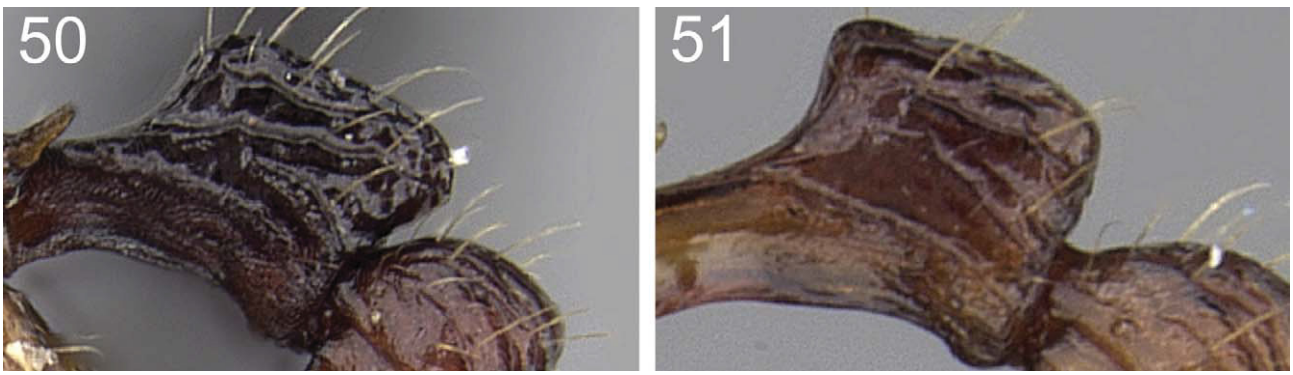
FIGURES 44–47. 44. *T. jedi* (CASENT0046064) petiolar node in dorsal view. **45.** *T. jedi* (CASENT0046064) petiolar node in profile. **46.** *T. avaratra* (CASENT0445167) petiolar node in dorsal view. **47.** *T. avaratra* (CASENT0445167) petiolar node in profile.

15. Propodeal spines very long (PSLI 37–44); petiolar node relatively lower (LPeI 63–73) and narrower (DPeI 111–118); petiolar dorsum strongly rugose (Fig. 48) . . . . . *Tetramorium pleganon*
- Propodeal spines long, but shorter than above (PSLI 27–37, usually below 34); petiolar node relatively higher (LPeI 54–66) and broader (DPeI 126–137); petiolar dorsum weakly rugose (Fig. 49) . . . . . *Tetramorium avaratra*



FIGURES 48 & 49. 48. *T. pleganon* (CASENT0280588) mesosoma and waist segments in profile. **49.** *T. avaratra* (CASENT0445167) mesosoma and waist segments in profile.

16. Posterodorsal corner of petiolar node strongly protruding posteriorly (Fig. 50) . . . . . *Tetramorium andohahela*
- Posterodorsal corner of petiolar node not protruding posteriorly (Fig. 51). 17



FIGURES 50 & 51. 50. *T. andohahela* (CASENT0484449) petiolar node in profile. **51.** *T. ala* (CASENT0038473) petiolar node in profile.

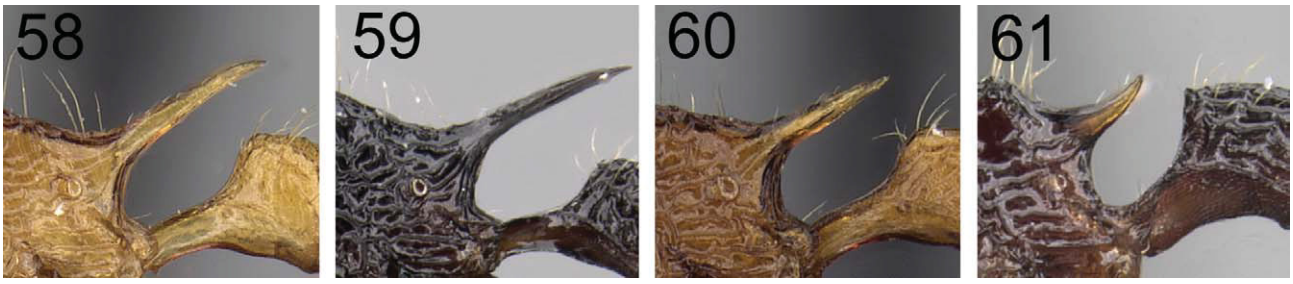
17. Eyes very small (OI 15–16); propodeal spines long (PSLI 28–33); anterodorsal margin of petiolar node situated slightly higher than posterodorsal margin; body orange to light reddish brown in colour (Fig. 52) . . . . . *Tetramorium isectum*
- Character combination never as above; if eyes small, then propodeal spines very long to extremely long (Figs. 53, 54) 18

FIGURES 52–54. 52. *T. isectum* (CASENT0172829) body in profile. **53.** *T. electrum* (CASENT0280589) body in profile. **54.** *T. andrei* (CASENT0102395) body in profile.

18. Petiolar node in profile comparatively high, between 1.3 to 1.6 times higher than long (LPeI 64–74); propodeal lobes strongly reduced and inconspicuous (Fig. 55). . . . . *Tetramorium electrum*
- Petiolar node in profile less high than above, between 1.1 times longer than high to 1.3 times higher than long (LPeI 76–105); propodeal lobes variably developed, usually conspicuous (Figs. 56, 57) 19

FIGURES 55–57. 55. *T. electrum* (CASENT0280850) mesosoma and petiole in profile. **56.** *T. elf* (CASENT0045788) mesosoma and petiole in profile. **57.** *T. ala* (CASENT0038473) mesosoma and petiole in profile.

19. Propodeal spines extremely long (PSLI 58–64) (Figs. 58, 59) 20
- Propodeal spines long to very long, but always significantly much shorter than above (PSLI 29–45) (Figs. 60, 61) 21



FIGURES 58–61. 58. *T. elf* (CASENT0045788) mesosoma in profile. **59.** *T. isoelectrum* (CASENT0152199) mesosoma in profile. **60.** *T. voasary* (CASENT0247162) mesosoma in profile. **61.** *T. nify* (CASENT0163155) mesosoma in profile.

20. Mandibles unsculptured, smooth, and shining; body colour yellow (Figs. 62, 63) . . . . . *Tetramorium elf*
- Mandibles noticeably longitudinally sculptured; body colour very dark brown to black (Fig. 64, 65) . . . *Tetramorium isoelectrum*

FIGURES 62–65. 62. *T. elf* (CASENT0045788) head in full-face view. **63.** *T. elf* (CASENT0045788) body in profile. **64.** *T. isoelectrum* (CASENT0152199) head in full-face view. **65.** *T. isoelectrum* (CASENT0152199) body in profile.

21. Petiolar node in dorsal view relatively long, always more than 1.3 times longer than wide (DPeI 72–76) (Fig. 66) . . *Tetramorium ala*
- Petiolar node in dorsal view relatively wider, always between 1.0 to approximately 1.2 times longer than wide (DPeI 82–98) (Figs. 67, 68) 22

FIGURES 66–68. 66. *T. ala* (CASENT0038473) petiolar node in dorsal view. **67.** *T. andrei* (CASENT0102395) petiolar node in dorsal view. **68.** *T. nify* (CASENT0163155) petiolar node in dorsal view.

22. Eyes relatively small (OI 16–17); propodeal spines relatively short (PSLI 29–30) (Fig. 69) . . . . . *Tetramorium nify*
- Eyes always much larger (OI 19–25); propodeal spines relatively longer (PSLI 32–45) (Figs. 70, 71) 23

FIGURES 69–71. 69. *T. nify* (CASENT0163155) body in profile. **70.** *T. andrei* (CASENT0102395) body in profile. **71.** *T. voasary* (CASENT0247162) body in profile.

23. Petiolar node with weakly defined and fairly rounded anterodorsal and posterodorsal margins; postpetiole relatively longer, longer than wide to slightly wider than long (DPpI 95–101) (Fig. 72). . . . . *Tetramorium voasary*
- Petiolar node with moderately to sharply defined anterodorsal and posterodorsal margins; postpetiole relatively wider, between 1.0 to 1.4 times wider than long (DPpI 103–136) (Fig. 73, 74) . . . . . *Tetramorium andrei*

FIGURES 72–74. 72. *T. voasary* (CASENT0247162) petiolar node in profile. **73.** *T. andrei* (CASENT0101821) petiolar node in profile. **74.** *T. andrei* (CASENT0163560) petiolar node in profile.

Tetramorium andrei species complex

This species complex is the largest within the *T. tortuosum* group with the nine species *T. ala*, *T. andohahela*, *T. andrei*, *T. elf*, *T. isectum*, *T. isoelectrum*, *T. electrum*, *T. nify*, and *T. voasary*. The forecoxae are usually completely or mostly unsculptured, smooth, and shining, although sculpture is sometimes present. What sculpture is present is mostly superficial and generally does not consist of strongly longitudinally arranged rugae. Instead, it is reticulate-punctate with few superimposed rugulae or traces of rugulae. In a few species (*e.g. T. elf*, *T. voasary*) the forecoxae are partly rugulose, but the sculpture is comparatively weak, and never covers the whole coxa as in the *T. smaug* species complex. The sculpture may appear longitudinal at first glance, but this is due to sections of linearly arranged reticulate-punctate sculpture, not true rugae/rugulae (e.g. *T. isoelectrum*). The first gastral tergite is always completely devoid of any sculpture, and fairly smooth and shining.

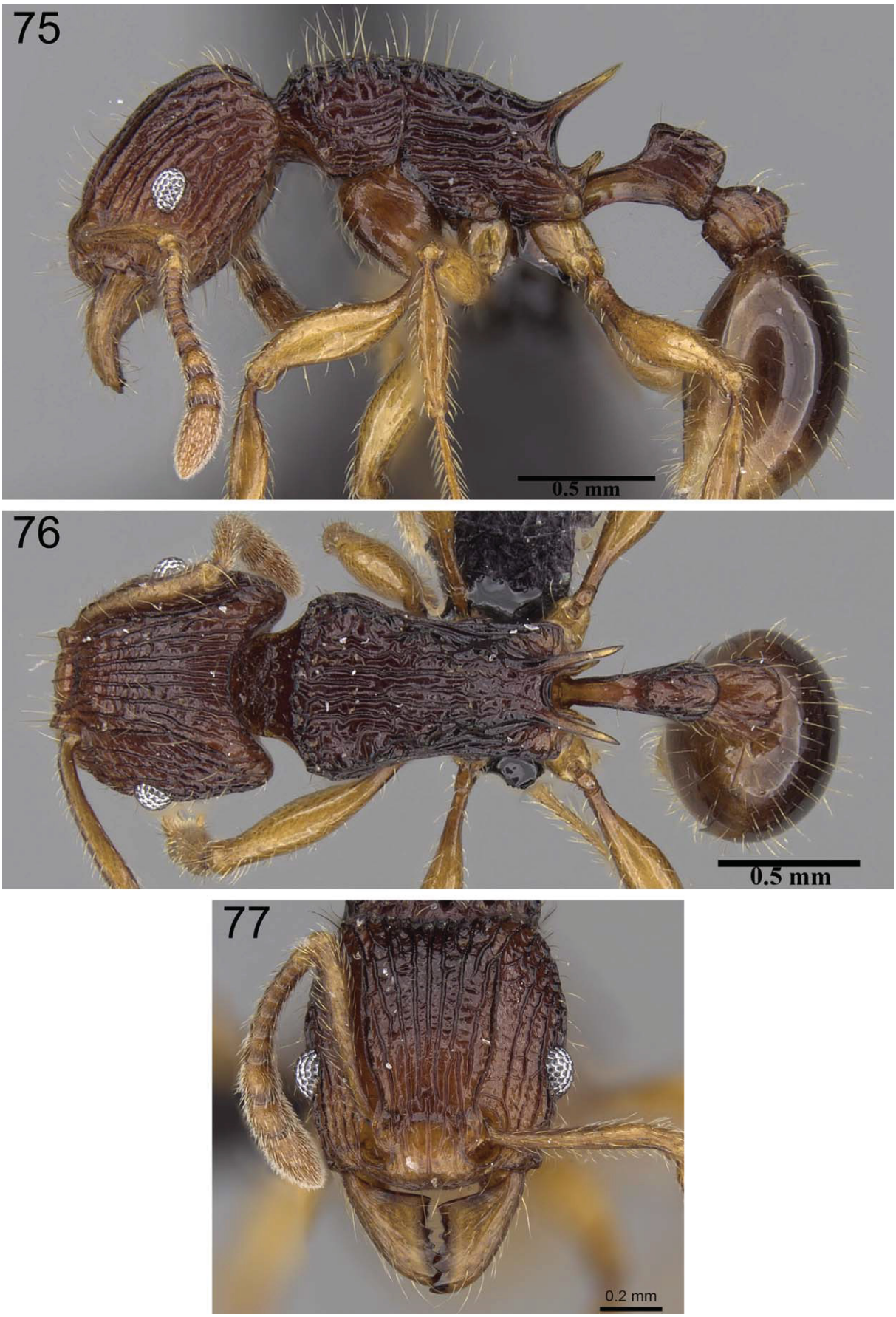
***Tetramorium ala* Hita Garcia & Fisher sp. n.**
(Figs. 51, 57, 66, 75, 76, 77, 141)

Holotype worker, MADAGASCAR, Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 15.17833 S, 49.635 E, 1100 m, montane rainforest, sifted litter (leaf mold, rotten wood), collection code BLF08150, 12.–16.III.2003 (*B.L. Fisher, C. Griswold et al.*) (CASC: CASENT0038473). Paratypes, 13 workers with same data as holotype (BMNH: CASENT0038387; CASC: CASENT0038371; CASENT0038374; CASENT0038389; CASENT0038410; CASENT0038414; CASENT0038453; CASENT0038459; CASENT0038464; CASENT0038467; MCZ: CASENT0038404; MHNG: CASENT0038423; NHMB: CASENT0038373); 1 worker with same data as holotype except sampled from ground and collection code BLF08230 (CASC: CASENT0497817); 9 workers with same data as holotype except sampled from root mat at ground layer and collection code BLF08185 (CASC: CASENT0498013; CASENT0498014; CASENT0498015).

Diagnosis
Tetramorium ala can be distinguished from the other *T. andrei* species complex members by the following combination of characters: eyes usually moderately sized (OI 20–21); propodeal spines long to very long (PSLI 38–42); petiolar node in dorsal view relatively slender and long, around 1.3 to 1.4 times longer than wide (DPeI 72–76); posterodorsal corner of petiolar node not strongly protruding posteriorly; body bright orange to light brown in colour.

Description
HL 0.88–1.01 (0.94); HW 0.83–0.96 (0.88); SL 0.69–0.76 (0.72); EL 0.17–0.19 (0.18); PH 0.43–0.49 (0.46); PW 0.63–0.74 (0.69); WL 1.16–1.29 (1.22); PSL 0.34–0.41 (0.37); PTL 0.29–0.34 (0.31); PTH 0.30–0.35 (0.32); PTW 0.21–0.26 (0.23); PPL 0.27–0.33 (0.30); PPH 0.30–0.36 (0.32); PPW 0.30–0.36 (0.32); CI 93–95 (94); SI 79–85 (81); OI 20–21 (20); DMI 54–58 (57); LMI 37–39 (38); PSLI 38–42 (40); PeNI 31–34 (33); LPeI 93–98 (95); DPeI 72–76 (75); PpNI 44–48 (46); LPpI 87–95 (92); DPpI 102–112 (107); PPI 135–143 (139) (12 measured).

Head distinctly longer than wide (CI 93–95). Posterior head margin concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, strongly diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, but shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively short to moderately long, not reaching posterior head margin (SI 79–85). Eyes short to moderately sized (OI 20–21). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–39). Propodeal spines long to very long, spinose, and acute (PSLI 38–42); propodeal lobes well-developed and comparatively long, elongate-triangular, and acute. Petiolar node in profile rectangular nodiform with sharply defined angles, between 1.0 to 1.1 times higher than long (LPeI 93–98), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum straight; node in dorsal view around 1.3 to 1.4 times longer than wide (DPeI 72–76). Postpetiole in profile globular to subglobular, approximately 1.1 times higher than long (LPpI 87–95); in dorsal view 1.0 to 1.1 times wider than long (DPpI 102–112). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view approximately 1.3 to 1.4 times wider than petiolar node (PPI 135–143). Mandibles distinctly longitudinally rugose; clypeus always with a very well-developed and pronounced longitudinal median ruga and few much weaker, and often broken lateral rugae/rugulae; cephalic dorsum between frontal carinae with seven to ten longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, rugae only very rarely with cross-meshes; lateral and ventral head usually longitudinally rugose, sometimes partly reticulate-rugose. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae usually completely unsculptured, smooth, and shiny, sometimes with partial superficial sculpture. Waist segments longitudinally rugose. Ground sculpture generally faint to absent everywhere on body. First gastral tergite unsculptured, smooth, and shining. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with suberect to erect standing hairs. Body colour uniformly bright orange to orange-brown.



FIGURES 75–77. *T. ala*, holotype (CASENT0038473). **75.** Body in profile. **76.** Body in dorsal view. **77.** Head in full-face view.

Notes
The new species is currently only known to occur in the type locality Montagne d'Anjanaharibe where it was sampled in montane rainforest at 1100 m elevation. Most specimens were found in leaf litter.

Tetramorium ala has the longest petiolar node in dorsal view within the species complex, which is around 1.3 to 1.4 times longer than wide (DPeI 72–76), whereas all other species (except *T. andohahela*) have much shorter and wider nodes (DPeI 82–114). *Tetramorium andohahela* also has a relatively long and slender node in dorsal view (DPeI 73–79), but the posterodorsal corner of the petiolar node distinctly protrudes posteriorly in this species, a character absent in *T. ala*. Not considering the node shape in dorsal view, *T. ala* is not easily confused with *T. electrum*, *T. elf*, or *T. isoelectrum* since the latter species have significantly smaller eyes (OI 16–19), much longer propodeal spines (PSLI 46–64), and much shorter propodeal lobes. The other two species with very small eyes, *T. isectum* (OI 15 -16) and *T. nify* (OI 16–17), are morphologically not very close to *T. ala* with its larger eyes (OI 20–21). Due to its fairly rounded anterodorsal and posterodorsal margins of the petiolar node, *T. voasary* can be easily separated from *T. ala*, which has very sharply defined margins. The last and most variable species of the complex, *T. andrei*, could be confused with *T. ala* since they share most morphological characters, especially in profile view. However, as mentioned above, the different node shape in dorsal view distinguishes them clearly (DPeI 72–76 in *T. ala* versus DPeI 82–98 in *T. andrei*).

Etymology
The species epithet is an arbitrary combination of letters.

Material examined
MADAGASCAR: Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 15.17833 S, 49.635 E, 1100 m, montane rainforest, 12.–16.III.2003 (*B.L. Fisher, C. Griswold et al.*).

Tetramorium andohahela **Hita Garcia & Fisher sp. n.**
(Figs. 50, 78, 79, 80, 141)

Holotype worker, MADAGASCAR, Toliara, Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 24.76389 S, 46.75167 E, 900 m, montane rainforest, sifted litter (leaf mold, rotten wood), collection code BLF05010, 21.–25.I.2002 (*B.L. Fisher, C. Griswold, et al.*) (CASC: CASENT0454449). Paratypes, 25 workers with same data as holotype (BMNH: CASENT0484441; CASC: CASENT0454555; CASENT0484356; CASENT0484390; CASENT0484395; CASENT0484407; CASENT0484417; CASENT0484430; CASENT0484433; CASENT0484434; CASENT0484435; CASENT0484472; CASENT0484482; CASENT0484487; CASENT0484488; CASENT0484489; CASENT0484494; CASENT0484499; CASENT0484508; CASENT0484520; CASENT0484524; MCZ: CASENT0484469; MHNG: CASENT0484510; NHMB: CASENT0484555).

Diagnosis
Tetramorium andohahela can be straightforwardly identified within the *T. andrei* species complex due to the very characteristic petiolar node shape with the posterodorsal corner strongly protruding posteriorly.

Description
HL 0.94–1.10 (1.02); HW 0.95–1.15 (1.05); SL 0.75–0.90 (0.83); EL 0.20–0.25 (0.22); PH 0.49–0.60 (0.53); PW 0.71–0.85 (0.78); WL 1.28–1.53 (1.40); PSL 0.44–0.58 (0.50); PTL 0.36–0.46 (0.42); PTH 0.37–0.48 (0.43); PTW 0.28–0.35 (0.32); PPL 0.32–0.36 (0.34); PPH 0.37–0.48 (0.43); PPW 0.40–0.48 (0.44); CI 101–106 (103); SI 76–82 (79); OI 20–22 (21); DMI 54–58 (56); LMI 37–40 (38); PSLI 45–53 (49); PeNI 38–43 (41); LPeI 93–105 (99); DPeI 73–80 (76); PpNI 55–59 (56); LPpI 76–88 (80); DPpI 121–137 (129); PPI 133–145 (139) (14 measured).

Head weakly to distinctly wider than long (CI 101–106); posterior head margin concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes short to moderate, not reaching posterior head margin (SI 76–82). Eyes of

moderate size (OI 20–22). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–40). Propodeal spines very long to extremely long, spinose and acute (PSLI 45–53); propodeal lobes well-developed, elongate-triangular, and acute. Petiolar node in profile rectangular nodiform with well-defined angles, weakly higher than long to weakly higher than long (LPeI 93–105), anterior and posterior faces almost parallel, anterior face much lower than posterior face, posterodorsal margin situated much higher than anterodorsal, posterior face weakly concave, posterodorsal corner strongly protruding posteriorly; node in dorsal view between 1.2 to 1.4 times longer than wide (DPeI 73–80). Postpetiole in profile subglobular, approximately 1.1 to 1.3 times higher than long (LPpI 76–88); in dorsal view around 1.2 to 1.4 times wider than long (DPpI 121–137). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view approximately 1.3 to 1.5 times wider than petiolar node (PPI 133–145). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose/rugulose, with four to seven rugae/rugulae, median ruga/rugula often developed and conspicuous, remaining rugae/rugulae often short or irregularly arranged; cephalic dorsum between frontal carinae with eight to ten longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted or with cross-meshes; lateral and ventral head mainly reticulate-rugose, less longitudinally rugose. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae usually unsculptured, smooth, and shining, rarely with superficial, weak sculpture. Waist segments mainly longitudinally rugose. Gaster completely unsculptured, smooth, and shining. Ground sculpture generally faint to absent everywhere on body. Body with numerous long, fine, standing hairs. Anterior edges of antennal scapes with suberect to erect hairs. Head, mesosoma, waist segments, and gaster brown to dark brown, mandibles, antennae, and legs of much lighter colour, usually yellow.

Notes

Tetramorium andohahela is only found in a strip of localities in southern-eastern Madagascar that ranges from the southernmost locality, Andohahela, north to Ranomafana. All localities are rainforests or montane rainforests located at elevations of 800 to 1250 m. Also, the species was mostly collected from leaf litter.

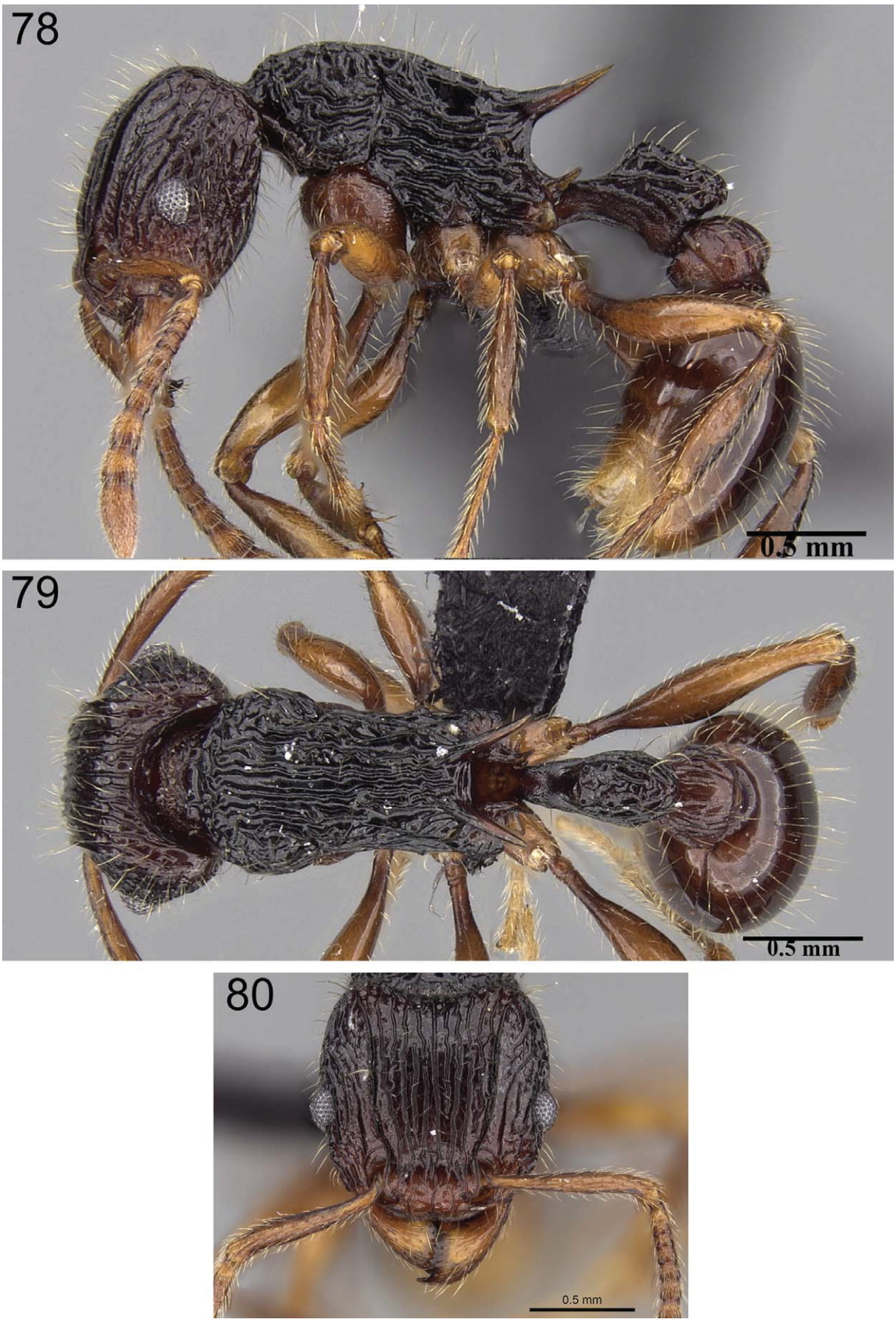
The petiolar node is somewhat variable in its length since it ranges from longer than wide to wider than long (LPeI 93–105). This is not of much diagnostic importance, however, since the node always retains its characteristic shape with the posterodorsal corner protruding strongly posteriorly. This extraordinary node shape is absent in the remainder of the *T. andrei* complex and the whole *T. tortuosum* group in Madagascar, making *T. andohahela* straightforwardly recognisable.

Etymology

The new species is named after the type locality, the Andohahela National Park, which harbours an extraordinary variety of landscapes and habitats, and is of special importance for the conservation of biodiversity in Madagascar. The species epithet is a noun in apposition, and thus invariant.

Material examined

MADAGASCAR: Fianarantsoa, 2 km W Andrambovato, along river Tatamaly, 21.51167 S, 47.41 E, 1075 m, montane rainforest, 3.–5.VI.2005 (*B.L. Fisher et al.*); Fianarantsoa, Rés. Andringitra, 43 km S Ambalavao, 22.23333 S, 47 E, 825 m, rainforest, 4.X.1993 (*B.L. Fisher*); Fianarantsoa, Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango,23.83517 S, 46.96367 E, 940 m, rainforest, 13.–15.XI.2006 (*B.L. Fisher et al.*); Fianarantsoa, Parc National Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, 23.84083 S, 46.9575 E, 1250 m, montane rainforest, 17.XI.2006 (*B.L. Fisher et al.*); Fianarantsoa, R.S. Ivohibe, 7.5 km ENE Ivohibe, 22.47 S, 46.96 E, 900 m, rainforest, 7.–12.X.1997 (*B.L. Fisher*); Fianarantsoa, 9.0 km NE Ivohibe, 22.42667 S, 46.93833 E, 900 m, rainforest, 12.–17.X.1997 (*B.L. Fisher*); Fianarantsoa, Parc Nationale Ranomafana, Talatakely, 21.24833 S, 47.42667 E, in guava forest, 9.–26.IV.1998 (*C. Griswold et al.*); Fianarantsoa, Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 21.29 S, 47.43333 E, 1100 m, montane rainforest, 27.–31.III.2003 (*B.L. Fisher, C. Griswold, et al.*); Toliara, Rés. Andohahela, 11 km NW Enakara, 24.56667 S, 46.83333 E, 800 m, rainforest, 16.XI.1992 (*B.L. Fisher*); Toliara,13 km NW Enakara, Rés. Andohahela, 24.55 S, 46.8 E, 1250 m, montane rainforest, 30.XI.1992 (*B.L. Fisher*); Toliara, Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 24.76389 S, 46.75167 E, 900 m, montane rainforest, sifted litter (leaf mold, rotten wood), collection code BLF05010, 21.–25.I.2002 (*B.L. Fisher, C. Griswold, et al.*).



FIGURES 78–80. *T. andohahela*, holotype (CASENT0484449). **78.** Body in profile. **79.** Body in dorsal view. **80.** Head in full-face view.

Tetramorium andrei Forel, 1892a

(Figs. 13, 54, 67, 70, 73, 74, 81, 82, 83, 141)

Tetramorium (Xiphomyrmex) andrei Forel, 1892a:263. Lectotype worker [designated here], MADAGASCAR, Toamasina, province de Bezanozano, Nosibé Village de I'Imerina (*M. Sikora*) (MHNG: CASENT0101821) [examined]. Paralectotypes, two workers with same data as holotype (MHNG: CASENT0101281; CASENT0101282) [examined]. [Combination in *Xiphomyrmex* by Wheeler, W.M. 1922:1031; in *Tetramorium* by Bolton, 1979:143].

Tetramorium (*Xyphomyrmex*) *andrei* st. *robustior* Forel, 1892b:521. Syntype workers, Foret d'Andrangoloaca (*M. Sikora*) (MHNG: CASENT0101279, CASENT0101280) [examined]. [Raised to species by Bolton, 1979:147]. **Syn. n.**

[Note: there is a bit of confusion concerning the type locality of *T. andrei*. The type locality information on the labels from MHNG is clearly "Nosibé Village del I'Imerina (*Sikora*)", whereas the description by Forel gives the type locality as "Environs de la ville d'Anosibé (province de Bezanozano), a trois journées a l'est-sud-est d'Antananarivo (M. Sikora)." There are several places with the names Nosibé or Anosibé in Madagascar, and additional information is necessary to ascertain which was meant by Forel. Since he mentioned that the locality was three days' march ESE of Antananarivo in the province of Bezanozano we can hypothesize that it might be close to present-day Anosibe an 'Ala in Toamasina, which is ESE of Antananarivo approximately 30 km south of Moramanga and in the traditional area of the Bezanozano people. Some uncertainty remains, but we think that this locality data is the closest to Forel's (1891) description.]

Diagnosis

Within the *T. andrei* species complex *T. andrei* is clearly identifiable based on the following character combination: eyes short to moderately sized (OI 19–25); propodeal spines long to very long (PSLI 32–45, usually below 40); in profile petiolar node with well-developed anterodorsal and posterodorsal angles, usually sharply defined, often one or both angles weakly rounded; posterodorsal corner of petiole not strongly protruding posteriorly; node in dorsal view ranging from as long as wide to 1.2 times longer than wide (DPeI 82–98); postpetiole in dorsal view as wide as long to approximately 1.4 times wider than long (DPpI 103–136); body colour ranging from uniform reddish-brown to very dark brown.

Description

HL 0.77–1.11 (0.95); HW 0.73–1.06 (0.91); SL 0.60–0.86 (0.70); EL 0.15–0.23 (0.20); PH 0.37–0.55 (0.47); PW 0.53–0.75 (0.67); WL 0.96–1.40 (1.20); PSL 0.27–0.46 (0.36); PTL 0.27–0.36 (0.32); PTH 0.29–0.45 (0.37); PTW 0.23–0.33 (0.28); PPL 0.26–0.37 (0.32); PPH 0.29–0.45 (0.37); PPW 0.30–0.44 (0.37); CI 91–100 (96); SI 68–86 (77); OI 19–25 (22); DMI 50–60 (56); LMI 37–43 (39); PSLI 32–45 (38); PeNI 36–48 (42); LPeI 76–97 (86); DPeI 82–98 (90); PpNI 48–63 (55); LPpI 75–98 (88); DPpI 103–136 (116); PPI 117–149 (131) (65 measured).

Head distinctly longer than wide to as long as wide (CI 91–100). Posterior head margin weakly concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively short to moderately long, not reaching posterior head margin (SI 68–86). Eyes short to moderately sized (OI 19–25). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–43). Propodeal spines long, rarely very long, spinose, and acute (PSLI 32–45, usually below 40); propodeal lobes variable, short and weakly developed to well-developed and moderately long, triangular to elongate-triangular, and rounded and blunt to acute. Petiolar node in profile rectangular nodiform with usually well-defined angles, node ranging from as high as long to 1.3 times higher than long (LPeI 76–97), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum straight to weakly convex, sometimes anterodorsal or posterodorsal margins slightly higher than other; node in dorsal view ranging from as long as wide to 1.2 times longer than wide (DPeI 82–98). Postpetiole in profile globular to subglobular, approximately as high as long to 1.3 times higher than long (LPpI 75–98); in dorsal view between as wide as long to approximately 1.4 wider than long (DPpI 103–136). Generally, postpetiole in profile approximately as voluminous as petiolar node, in dorsal view postpetiole approximately 1.2 to 1.5 times wider than petiolar node (PPI 117–149). Mandibles usually distinctly longitudinally rugose, in some localities mandibles weakly sculptured to completely unsculptured, smooth, and shining; clypeus usually longitudinally rugose/rugulose, almost always with one distinct median ruga/rugula, often two well-developed rugae/rugulae laterally, sometimes only median ruga/rugula distinct and remaining sculpture irregularly arranged; cephalic dorsum between frontal carinae with 7 to 12 longitudinal rugae running from posterior head

margin to posterior clypeus, rugae often broken, rarely with cross-meshes; lateral and ventral head mainly reticulate-rugose and to lesser extent longitudinally rugose. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae usually completely unsculptured, smooth, and shiny, sometimes with partial superficial sculpture. Waist segments longitudinally to irregularly rugose. Generally ground sculpture faint to absent everywhere on body, rarely head with weak to moderate reticulate-punctate ground sculpture. First gastral tergite unsculptured, smooth, and shining. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with subdecumbent to erect standing hairs. Body colour ranging from uniform reddish-brown (most commonly encountered) to very dark brown, often appendages of much lighter colour.

Notes

Tetramorium andrei is a widespread and common species found in most of the rainforests and montane rainforests of eastern and northern Madagascar. The southernmost locality is Andohahela in the southeast, and from there it ranges in an almost continuous band north to Montagne Francais in the northern tip of Madagascar. Fairly isolated from the main distribution, *T. andrei* is also encountered in Ambohijanahary and further north in Manongarivo and Ampasindava. The species was sampled at elevations from 10 to 1625 m, and lives in leaf litter.

It must be pointed out that *T. andrei* displays an extraordinary level of intraspecific variation, and we are confident that the material included under this name consists of three to four "good" species that we are unfortunately unable to delimit in this study. The morphometric range outlined above, based on 65 measured specimens, shows a remarkable variability not found in another Afrotropical or Malagasy *Tetramorium*. There are a number of characters that are variably developed, often within the same locality, which do not allow a consistent species delimitation. The most important characters are head shape (CI 91–100), antennal scape length (SI 68–86), the development of the propodeal lobes and the petiolar node, and the sculpture on the mandibles. There seem to be three to four relatively discrete groups that can be recognised by morphometrics and few important characters.

The first group is found in the southeast from Andohahela north to Andringitra, and is mainly characterised by relatively short antennal scapes (SI 68–74), short, rounded propodeal lobes, and a petiolar node without very sharply defined antero- and posterodorsal margins. The second group, which contains the type material of *T. andrei*, has significantly longer antennal scapes (SI 80–86), short but acute propodeal lobes, and a petiolar node with very well-developed and sharply defined antero- and posterodorsal margins. This group is mainly found in central-eastern Madagascar from Vevembe and Vatovavy north to Mandrisy. The third group contains the types of the junior synonym *T. robustior*, and is found from central-eastern to north-eastern Madagascar. It is characterised by comparatively longer antennal scapes (SI 80–85), longer, elongate-triangular, and very acute propodeal lobes, and a petiolar node with the posterodorsal margin weakly higher and more angular than the anterodorsal margin. The head in this group shows the widest shape with a CI approaching 100. The last group seems restricted to northern parts of Madagascar and is encountered north of Manongarivo in the West and Marotandrano in the east. In this group the mandibles are often unsculptured or almost unsculptured, and generally very smooth and shining. Also, the antennal scapes are relatively short (SI 70–77), the propodeal lobes are short, triangular, and often blunted, and the petiolar node has less strongly marginate antero- and posterodorsal margins. Sometimes, especially in Manongarivo, the anterodorsal margin of the petiole is situated slightly higher, although this is not consistent in that series.

Despite encountering these four groups within the extensive material of *T. andrei* examined during this study, we are reluctant to describe these as different species at the moment, even though some or all likely deserve species status. We observed that several of the characters mentioned above show a gradual overlap from one group to another, and it was not possible to draw significant lines between these groups recognisable for non-taxonomists to describe them as distinct species. Therefore, even though we examined several hundred specimens, we postpone a solution to this species delimitation problem within *T. andrei*. We are still confident that there are several more or less cryptic species involved, and for future studies we recommend measuring significantly more specimens than the 65 measured here. Morphometrics appears to be of high importance to find species limits, and might be a useful means to solve this problem. Molecular data, if possible from multiple genes, may also be necessary to support morphological and morphometric diagnostics.

Within the species complex, *T. andrei* is not characterised and distinguishable by specialised characters, but instead by their lack. *T. andrei* (OI 19–25, usually above 20) differs strikingly from the two species with very small

eyes: *T. isectum* (OI 15–16) and *T. nify* (OI 16–17). Furthermore, *T. andrei* can be easily distinguished from *T. electrum*, *T. elf*, and *T. isoelectrum* based on their smaller eyes (16–19), very long to extremely long propodeal spines (PSLI 46–64), and different body colours. *Tetramorium electrum* and *T. isoelectrum* are very dark brown to black and *T. elf* is of whitish to yellowish colour, and even though *T. andrei* shows a wide variation in colour, it is almost never yellowish as *T. elf* or as darkly coloured as *T. electrum* and *T. isoelectrum*. In addition, *T. andohahela* with its very distinctive petiolar node with the posterodorsal corner strongly protruding posteriorly cannot be misidentified with *T. andrei*, which does not have a node shape like that. *Tetramorium ala*, however, can be confused with *T. andrei*. They are both morphologically fairly similar, and in profile view almost indistinguishable. Nevertheless, in dorsal view they can be clearly separated from each other since the petiolar node of *T. ala* is much longer and thinner (DPeI 72–76) than that of *T. andrei* (DPeI 82–98). The last species of the complex, *T. voasary*, is morphologically also comparatively close to *T. andrei*. Their separation is based on the shape differences of both waist segments. In *T. andrei* the petiolar node in lateral view usually has very well defined, almost sharp, anterodorsal and posterodorsal margins, although they are often moderately rounded, and the postpetiole in dorsal view is between 1.0 to 1.4 times wider than long (DPpI 103–136). In contrast, the petiolar node of *T. voasary* has anterodorsal and posterodorsal margins that are fairly rounded, and a relatively longer postpetiole which is slightly longer than wide to slightly wider than long (DPpI 95–101).

Material examined

MADAGASCAR: Antananarivo, 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 18.4733 S, 47.96 E, 1300 m, montane rainforest, 5.–13.XII.2000 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Parc Nat. Mont. d'Ambre, 1000–1100 m, wet forest, 12.II.1977 (*W.L. & D.E. Brown*); Antsiranana, Parc National Montagne d'Ambre [1st campsite], 12.5144 S, 49.1814 E, 960 m, rainforest, 21.–26.I.2001 (*M.E. Irwin, E. Schlinger & R. Harin'Hala*); Antsiranana, Parc National Montagne d'Ambre [Petit Lac road], 12.5203 S, 49.1792 E, 1125 m, rainforest, 29.I.–11.II.2001 (*R. Harin'Hala*); Antsiranana, Parc National Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 12.5964 S, 49.1595 E, 1300 m, montane rainforest, 2.–7.II.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 12.5344 S, 49.1795 E, 925 m, 20.–26.I.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Parc National Montagne d'Ambre, Lac Maudit, 12.585 S, 49.1515 E, 1250 m, montane rainforest, 14.XI.2007 (*B.L. Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, Ambre Grand Lac, 12.5966 S, 49.1593 E, 1350 m, 13.XI.2007 (*B.L. Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, Antomboka, 12.5127 S, 49.1781 E, 970 m, 17.XI.2007 (*B.L. Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, Pic Bades, 12.5186 S, 49.1862 E, 900 m, montane rainforest, 20.XI.2007 (*B.L. Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5139 S, 49.1778 E, 984 m, montane rainforest, 28.II.2011 (*B.L. Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5178 S, 49.1796 E, 1000 m, 4.–7.III.2011 (*B.L. Fisher et al.*); Antsiranana, Parc National Montagne d'Ambre, 12.5286 S, 49.1772 E, 1100 m, 12.III.2011 (*B.L. Fisher et al.*); Antsiranana, Ampasindava, Forêt d'Ambilanivy, 3.9 km 181° S Ambaliha, 13.7986 S, 48.1617 E, 600 m, 4.–9.III.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, 11.0 km WSW Befingotra, Rés. Anjanaharibe-Sud, 14.75 S, 49.45 E, 1550 m, montane rainforest, 18.XI.1994 (*B.L. Fisher*); Antsiranana, Betaolana Forest, along Bekona River, 14.53 S, 49.4404 E, 880 m, rainforest, 4.III.2009 (*B.L. Fisher et al.*); Antsiranana, Forêt de Binara, 9.4 km 235° SW Daraina, 13.2633 S, 49.6 E, 1100 m, montane rainforest, 5.XII.2003 (*B.L. Fisher*); Antsiranana, Makirovana forest, 14.1667 S, 49.95 E, 715 m, rainforest, 1.–2.V.2011 (*B.L. Fisher et al.*); Antsiranana, R.S. Manongarivo, 12.8 km 228° SW Antanambao, 13.9767 S, 48.4233 E, 780 m, rainforest, 11.X.1998 (*B.L. Fisher*); Antsiranana, R.S. Manongarivo, 14.5 km 220° SW Antanambao, 13.9983 S, 48.4283 E, 1175 m, montane rainforest, 20.X.1998 (*B.L. Fisher*); Antsiranana, R.S. Manongarivo, 10.8 km 229° SW Antanambao, 13.9617 S, 48.4333 E, 400 m, rainforest, 8.XI.1998 (*B.L. Fisher*); Antsiranana, RNI Marojejy, 10.5 km NW Manantenina, 14.4333 S, 49.75 E, 1625 m, 6.–12.XI.1996 (*E.L. Quinter*); Antsiranana, Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 14.4433 S, 49.7433 E, 1325 m, montane rainforest, 19.III.2003 (*B.L. Fisher*); Antsiranana, Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, 15.–18.XI.2003 (*B.L. Fisher et al.*); Parc National de Marojejy, 25.7 km 32° NNE Andapa, 10.3 km 314° NW Manantenina, 14.445 S, 49.7417 E, 1575 m, montane rainforest, 21.XI.2003 (*B.L. Fisher*); Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, 14.XII.2005 (*B.L. Fisher et al.*); Fianarantsoa, Foret d'Ambalagoavy Nord, Ikongo, Ambatombe, 21.8275 S, 47.3389 E, 625 m, 1.XII.2000 (*R. Harin'Hala & M.E. Irwin*); Fianarantsoa, 45km S. Ambalavao, 22.2167 S, 47.0167 E, 785 m, rainforest,

24.–25.IX.1993 (*B.L. Fisher*); Fianarantsoa, 43 km S Ambalavao, Rés. Andringitra, 22.2333 S, 47 E, 825 m, rainforest, 5.X.1993 (*B.L. Fisher*); Fianarantsoa, R.S. Ivohibe, 7.5 km ENE Ivohibe, 22.47 S, 46.96 E, 900 m, rainforest, 7.–12.X.1997 (*B.L. Fisher*); Fianarantsoa, Réserve Speciale Manombo 24.5 km 228° Farafangana, 23.0158 S, 47.719 E, 30 m, rainforest, 20.–22.IV.2006 (*B.L. Fisher et al.*); Fianarantsoa, Forêt Classée Vatovavy, 7.6 km 122º Kianjavato, 21.4 S, 47.94 E, 175 m, rainforest, 6.–8.VI.2005 (*B.L. Fisher et al.*); Fianarantsoa, Forêt de Vevembe, 66.6 km 293° Farafangana, 22.791 S, 47.1818 E, 600 m, rainforest, transition to montane forest, 23.–24.IV.2006 (*B.L. Fisher et al.*); Mahajanga, Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, 16.2832 S, 48.8144 E, 865 m, transitional humid forest, 6.–8.XII.2007 (*B.L. Fisher et al.*); Toamasina, Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 15.2883 S, 49.5483 E, 600 m, 17.–21.III.2003 (*B.L. Fisher, C. Griswold et al.*); Toamasina, 6.3 km S Ambanizana, Andranobe, 15.6813 S, 49.958 E, 25 m, rainforest, 13.–23.XI.1993 (*B.L. Fisher*); Toamasina, 6.9 km NE Ambanizana, Ambohitsitondroina, 15.5667 S, 50 E, 825 m, rainforest, 2.XII.1993 (*B.L. Fisher*); Toamasina, Ambanizana, Parc National Masoala, 15.5722 S, 50.0069 E, 1020 m, montane rainforest, 2.–6.III.2003 (*D. Andriamalala, D. Silva et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.7727 S, 49.2655 E, 450 m, rainforest, 20.–22.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.7633 S, 49.2669 E, 520 m, rainforest, 22.–24.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.8175 S, 49.295 E, 360 m, rainforest, 25.–27.II.2010 (*B.L. Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8496 S, 48.2947 E, 1010 m, montane rainforest, 3.–6.III.2007 (*B.L. Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8477 S, 48.2957 E, 1000 m, montane rainforest, 5.–8.III.2007 (*B.L. Fisher et al.*); Toamasina, Amparihibe, 15° 2' S, 49° 34' E, II.–III.2003 (*K.A. Jackson & D. Carpenter*); Toamasina, Analamay, 18.8062 S, 48.3371 E, 1068 m, montane rainforest, 21.III.2004 (*Malagasy ant team*); Toamasina, Station forestière Analamazaotra, Analamazaotra 1.3 km S Andasibe, 18.3847 S, 48.4127 E, 980 m, montane rainforest, 11.–13.XII.2007 (*B.L. Fisher et al.*); Toamasina, Forêt d'Analava Mandrisy, 5.9 km 195º Antanambe, 16.4857 S, 49.847 E, 10 m, littoral rainforest, 13.XI.2005 (*B.L. Fisher et al.*); Toamasina, 6 km ESE Andasibe (= Perinet), 18.95 S, 48.4667 E, 900 m, 17.XI.1990 (*P.S. Ward*); Toamasina, F.C. Andriantantely, 18.695 S, 48.8133 E, 530 m, 4.–10.XII.1998 (*H.J. Ratsirarson*); Toamasina, Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 15.1883 S, 49.615 E, 470 m, rainforest, 8.–12.III.2003 (*B.L. Fisher, C. Griswold et al.*); Toamasina, Reserve Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 17.924 S, 49.1997 E, 390 m, rainforest, 28.XI.2005 (*B.L. Fisher et al.*); Toamasina, Reserve Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 17.8867 S, 49.2025 E, 520 m, rainforest, 1.–3.XII.2005 (*B.L. Fisher et al.*); Toamasina, F.C. Didy, 18.1983 S, 48.5783 E, 960 m, rainforest, 16.–23.XII.1998 (*H.J. Ratsirarson*); Toamasina, Parc National Mananara-Nord, 7.1 km 261° Antanambe, 16.455 S, 49.7875 E, 225 m, rainforest, 14.XI.2005 (*B.L. Fisher et al.*); Toamasina, P.N. Mantadia, 18.7917 S, 48.4267 E, 895 m, rainforest, 28.XI.–1.XII.1998 (*H.J. Ratsirarson*); Toamasina, Nosibé Village de l'Imerina, province de Bezanozano (*M. Sikora*); Toamasina, Nosy Mangabe, 15° 30' S, 49° 46' E, 300 m, rainforest, 18.IV.1989 (*P.S. Ward*); Toamasina, Tamatave, Ampasimbe, 450 m, rainforest (*J.M. Betsch*); Toamasina, S.F. Tampolo, 10 km NNE Fenoarivo Atn., 17.2825 S, 49.43 E, 10 m, littoral rainforest, 10.IV.1997 (*B.L. Fisher*); Toamasina, Parcelle K9 Tampolo, 17.175 S, 49.268 E, 10 m, littoral forest, 19.IV.2004 (*Malagasy ant team*); Toamasina, Torotorofotsy, 18.8708 S, 48.3474 E, 1070 m, montane rainforest, marsh edge, 24.III.2004 (*Malagasy ant team*); Toamasina, Parc National de Zahamena, Tetezambatana forest, near junction of Nosivola and Manakambahiny Rivers, 17.743 S, 48.7294 E, 860 m, rainforest, 18.–19.II.2009 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena, 17.7336 S, 48.7262 E, 950 m, rainforest, 19.II.2009 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena, Besaky River, 17.7524 S, 48.8532 E, 760 m, rainforest, 22.II.2009 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena, Onibe River, 17.7591 S, 48.8547 E, 780 m, rainforest, 21.–23.II.2009 (*B.L. Fisher et al.*); Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18.26 S, 45.4183 E, 1100 m, montane rainforest, 13.–17.I.2003 (*B.L. Fisher, C. Griswold et al.*); Toliara, Rés. Andohahela, 11 km NW Enakara, 24.5667 S, 46.8333 E, 800 m, rainforest, 16.XI.1992 (*B.L. Fisher*); Toliara, Rés. Andohahela, 10 km NW Enakara, 24.5667 S, 46.8167 E, 430 m, rainforest, 22.XI.1992 (*B.L. Fisher*); Toliara, Rés. Andohahela, 6 km SSW Eminiminy, 24° 44' S, 46° 48' E, 330 m, rainforest, 4.II.1993 (*P.S. Ward*); Toliara, Parc National d'Andohahela, Manampanihy River, 5.4 km 113° ESE Mahamavo, 36.7 km 343° NNW Tolagnaro, 24.7639 S, 46.7668 E, 650 m, rainforest, 24.I.2002 (*B.L. Fisher et al.*); Toliara, Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 24.7585 S, 46.8537 E, 275 m, rainforest, 22.–24.XI.2006 (*B.L. Fisher et al.*); Toliara, Forêt Ivohibe 55.0 km N Tolagnaro, 24.569 S, 47.204 E, 200 m, rainforest, 2.–4.XII.2006 (*B.L. Fisher et al.*); Toliara, Grand Lavasoa, 25.9 km W Tolagnaro, 25.0877 S, 46.749 E, 450 m, rainforest, 30.XI.–2.XII.2006 (*B.L. Fisher et al.*); Toliara, 2.7 km WNW 302° Ste. Luce, 24.7717 S, 47.1717 E, 20 m, littoral rainforest, 9.–11.XII.1998 (*B.L. Fisher*).

FIGURES 81–83. *T. andrei*, lectotype (CASENT0484449). **81.** Body in profile. **82.** Body in dorsal view. **83.** Head in full-face view.

Tetramorium electrum Bolton, 1979

(Figs. 31, 53, 55, 84, 85, 86, 141)

Tetramorium electrum Bolton, 1979:144. Holotype worker, MADAGASCAR, Rte d'Anosibe, km 33, forest humus and litter, AB 44, 4.–12.IV.1975 (*A. Peyrieras*) (MCZ: CASENT0280589) [examined]. Paratypes, 11 workers with same data as holotype, and one worker from vic. Andasibe (= Perinet) 950–980 m, 2.–6.II.1977 (*W.L. & D.E. Brown*) (BMNH: CASENT0102350; MCZ: CASENT0280850; MCZ_paratype_32378) [examined].

Diagnosis

Tetramorium electrum is easily recognisable within the *T. tortuosum* group in the Malagasy region due to the following combination of characters: propodeal spines very long to extremely long (PSLI 46–52); petiolar node around 1.3 to 1.6 times higher than long (LPeI 64–74); posterodorsal corner of petiole not strongly protruding posteriorly; body dark brown to black in colour.

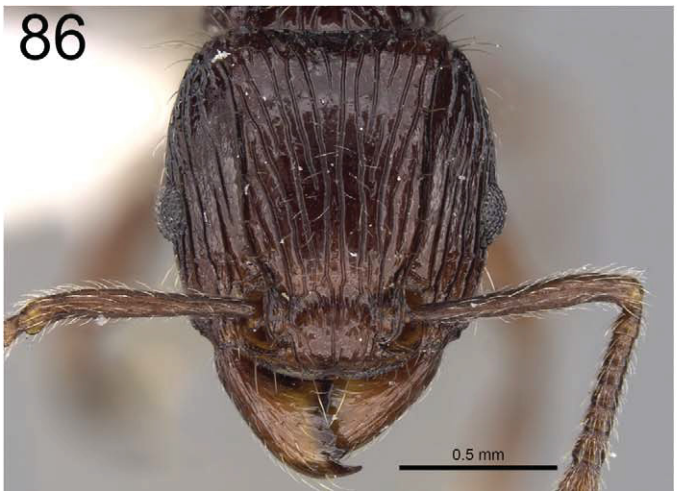
Description

HL 0.89–1.20 (1.07); HW 0.87–1.25 (1.08); SL 0.65–0.84 (0.77); EL 0.16–0.22 (0.19); PH 0.49–0.63 (0.55); PW 0.63–0.82 (0.75); WL 1.14–1.59 (1.34); PSL 0.44–0.60 (0.53); PTL 0.28–0.35 (0.31); PTH 0.38–0.47 (0.44); PTW 0.29–0.37 (0.33); PPL 0.32–0.40 (0.36); PPH 0.38–0.48 (0.43); PPW 0.37–0.44 (0.40); CI 98–104 (100); SI 67–74 (71); OI 16–19 (17); DMI 52–58 (56); LMI 39–44 (41); PSLI 46–52 (50); PeNI 41–46 (44); LPeI 64–74 (71); DPeI 100–114 (105); PpNI 50–59 (53); LPpI 77–89 (84); DPpI 106–116 (110); PPI 115–128 (122) (20 measured).

Head approximately as long as wide (CI 98–104). Anterior clypeal margin medially impressed. Posterior head margin weakly to moderately concave. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes very short, not reaching posterior head margin (SI 67–74). Eyes small (OI 16–19). Mesosomal outline in profile weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 39–44). Propodeal spines very long, spinose, and acute (PSLI 46–52); propodeal lobes strongly reduced, generally vestigial, sometimes very short, broadly triangular and blunt. Petiolar node in profile rectangular nodiform with moderately to sharply defined margins, around 1.3 to 1.6 times higher than long (LPeI 64–74), anterior and posterior faces often not parallel narrowing towards dorsum, anterodorsal and posterodorsal margins generally at approximately same height, dorsum straight to weakly convex, sometimes anterodorsal margin slightly higher than posterodorsal with dorsum tapering weakly backwards posteriorly; node in dorsal view as wide as long to 1.2 times wider than long (DPeI 100–114). Postpetiole in profile subglobular, approximately 1.1 to 1.3 times higher than long (LPpI 77–89); in dorsal view around 1.1 times wider than long (DPpI 106–116). Postpetiole in profile usually appearing a bit more voluminous than petiolar node, in dorsal view approximately 1.1 to 1.3 times wider than petiolar node (PPI 115–128). Mandibles ranging from completely unsculptured, smooth, and shining to finely striate, often partly striate and partly smooth; clypeus with three to six longitudinal rugulae, rugulae often broken and irregularly arranged; cephalic dorsum between frontal carinae with 8 to 12 longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, rugae only very rarely with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose with few cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose, often rugae on lateral mesosoma more irregularly arranged than on the dorsum. Forecoxae usually unsculptured, smooth, and shining, sometimes with superficial sculpture, rarely weakly reticulate-punctate or reticulate-rugulose. Waist segments with reticulate-rugose/rugulose to longitudinally rugose/rugulose sculpture, often weaker laterally. Ground sculpture everywhere on body faint to absent. First gastral tergite unsculptured, smooth, and shining. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. First gastral tergite without appressed pubescence. Anterior edges of antennal scapes with decumbent to erect standing hairs. Body very dark brown to black in colour, sometimes of lighter brown.

Notes

Tetramorium electrum is one of the most common and conspicuous genus members encountered in the eastern rainforests of Madagascar. Its distribution ranges from Andohahela in the southeast to Marojejy in the northeast. It is found at elevations from 25 to 1080 m, and appears to prefer the leaf litter stratum.



FIGURES 84–86. *T. electrum*, holotype (CASENT0280589). **84.** Body in profile. **85.** Body in dorsal view. **86.** Head in full-face view.

Within the species complex *T. electrum* can be grouped together with *T. elf* and *T. isoelectrum* on the basis of shared morphology. *Tetramorium elf* is not easily confused with *T. electrum*, however, since the first is yellowish in colour with longer antennal scapes (SI 78–83) and petiolar node (DPeI 88–96), whereas T. *electrum* is very dark brown to black in colour and the scapes and petiolar node are shorter (SI 67–74; DPeI 100–114). The head of *T. elf* (CI 92–96) is also narrower than that of *T. electrum* (CI 98–104). More challenging is the separation of *T. electrum* from *T. isoelectrum* since they are superficially very similar. Much like *T. elf*, *T. isoelectrum* also has longer antennal scapes (SI 81–84), a longer petiolar node (DPeI 87–97), and a less broad head (CI 93–96) compared to *T. electrum*. Another difference is the petiolar node, which is lower and more square in *T. isoelectrum* (LPeI 77–86) but higher and narrows towards the dorsum in *T. electrum* (LPeI 64–74). Furthermore, *T. electrum* is not likely to be misidentified with the remaining species of the complex due to the combination of very long to extremely long propodeal spines (PSLI 46–52), low and inconspicuous propodeal lobes, and comparatively high petiolar node.

The general similarity between *T. electrum* and *T. isoelectrum* offers the slight possibility that they may belong to the same species; however, this does not seem likely given the material examined in this study. *Tetramorium electrum* is very common and we were able to examine several hundred specimens. Despite the variation mentioned below, the species seems to be relatively consistent throughout its range in eastern Madagascar. *Tetramorium isoelectrum* is less common and only found in northeastern Madagascar, mostly north of the distribution range of *T. electrum*. However, both species overlap in their distribution ranges and they are found in sympatry in Marojejy. There, both species retain their species-specific characteristics, and can be distinguished using the diagnostic notes provided in this revision. This piece of biogeographic evidence, in combination with the significant morphometric differences between the two species, provides strong support for their heterospecificity.

It must be noted that some morphological variation exists within *T. electrum*. This fact is not surprising considering its large distribution range in eastern Madagascar. The mandibles are usually finely striate, but some populations have completely unsculptured mandibles while only partly sculptured mandibles are found in other series. The shape of the petiolar node is also somewhat variable. The node is usually rectangular nodiform but comparatively high. In many specimens the anterodorsal margin is slightly higher than the posterodorsal, which causes the dorsum to taper backwards, even if weakly (as in the holotype CASENT0280589). In other specimens the node narrows distinctly towards the dorsum but with the anterior and posterior faces almost mirror-inverted (like in the paratype specimens CASENT0102350 and CASENT0280850).

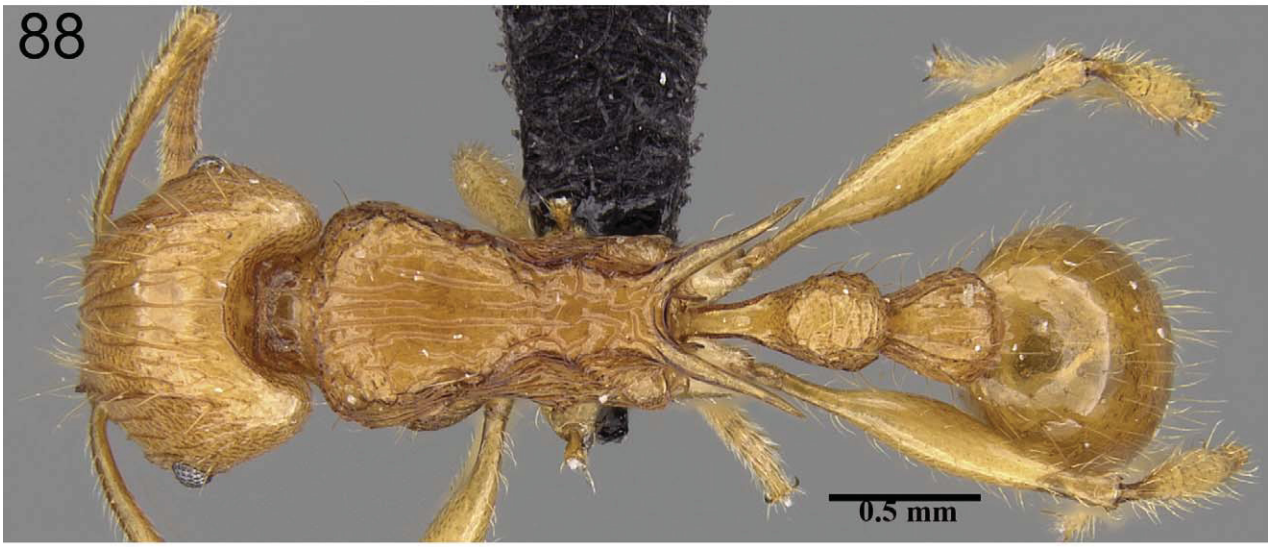
Material examined

MADAGASCAR: Antsiranana, Marojejy National Park, Sambava district, 5 km W of Manantenina village, 1st Camp site (Mantella), 14.4382 S, 49.774 E, 487 m, low altitude rainforest, 28.IV.–7.V.2005 (*Rin'Ha & Mike*); Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14.4367 S, 49.775 E, 450 m, rainforest, 12.–15.XI.2003 (*B.L. Fisher et al.*); Antsiranana, Masoala Peninsula, Ambavoany Forest, 15° 12' 28.7" S, 50° 17' 20" E, 30 m, primary rainforest, 26.IV.1996 (*G.D. Alpert et al.*); Fianarantsoa, 45 km S. Ambalavao, 22.2167 S, 47.0167 E, 785 m, rainforest, 24.–25.IX.1993 (*B.L. Fisher*); Fianarantsoa, Rés. Andringitra, 43 km S Ambalavao, 22.2333 S, 47 E, 825 m, rainforest, 4.–5.X.1993 (*B.L. Fisher*); Fianarantsoa, Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, 23.8352 S, 46.9637 E, 940 m, rainforest, 14.XI.2006 (*B.L. Fisher et al.*); Fianarantsoa, 9.0 km NE Ivohibe, 22.4267 S, 46.9383 E, 900 m, rainforest, 12.–17.XI.1997 (*B.L. Fisher*); Fianarantsoa, Réserve Speciale Manombo 24.5 km 228° Farafangana, 23.0158 S, 47.719 E, 30 m, rainforest, 20.IV.2006 (*B.L. Fisher et al.*); Fianarantsoa, Ranomafana Nat. Park, Ambohila, 21° 10' 9" S, 47° 33' 7" E, 700 m, montane rainforest, 23.VII.1992 (*A. Kingman*); Fianarantsoa, Ranomafana Nat. Park, Miaranony forest, 700 m, montane rainforest, 26.X.1992 (*E. Raferiarison*); Fianarantsoa, P.N. Ranomafana, Tolongoina-Ampasimpotsy, 21.4799 S, 47.5571 E, 577 m, rainforest, 13.III.–1.IV.2003 (*V. Clark*); Fianarantsoa, Forêt Classée Vatovavy, 7.6 km 122º Kianjavato, 21.4 S, 47.94 E, 175 m, rainforest, 6.–8.VI.2005 (*B.L. Fisher et al.*); Fianarantsoa, Forêt de Vevembe, 66.6 km 293° Farafangana, 22.791 S, 47.1818 E, 600 m, rainforest, transition to montane forest, 23.IV.2006 (*B.L. Fisher et al.*); Mahajanga, Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, 16.2832 S, 48.8144 E, 865 m, transition humid forest, 6.–8.XII.2007 (*B.L. Fisher et al.*); Toamasina, Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 15.2883 S, 49.5483 E, 600 m, rainforest, 17.–21.III.2003 (*B.L. Fisher, C. Griswold et al.*); Toamasina, 6.3 km S Ambanizana, Andranobe, 15.6813 S, 49.958 E, 25 m, rainforest, 15.XI.1993 (*B.L. Fisher*); Toamasina, 6.9 km NE Ambanizana, Ambohitsitondroina, 15.5667 S, 50 E, 825 m, rainforest, 2.–8.XII.1993 (*B.L. Fisher*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7727 S, 49.2655 E, 450 m, rainforest, 20.–22.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.7691 S, 49.267 E, 475 m, rainforest,

21.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.7633 S, 49.2669 E, 520 m, rainforest, 22.–24.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.7702 S, 49.2664 E, 470 m, rainforest, 23.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.7674 S, 49.2681 E, 500 m, rainforest, 23.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.8175 S, 49.295 E, 360 m, rainforest, 25.–27.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.8121 S, 49.2922 E, 460 m, rainforest, 26.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.8174 S, 49.2925 E, 400 m, rainforest, 26.II.2010 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.8056 S, 49.2951 E, 480 m, rainforest, 27.II.2010 (*B.L. Fisher et al.*); Toamasina, Forêt Ambatovy, 14.3 km 57° Moramanga, 18.8508 S, 48.32 E, 1075 m, montane rainforest, 18.XII.2004 (*B.L. Fisher*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8496 S, 48.2947 E, 1010 m, montane rainforest, 3.–6.III.2007 (*B.L. Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8394 S, 48.3084 E, 1080 m, montane rainforest, 4.–8.III.2007 (*B.L. Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8477 S, 48.2957 E, 1000 m, montane rainforest, 5.–8.III.2007 (*B.L. Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8581 S, 48.2849 E, 1040 m, montane rainforest, 5.–8.III.2007 (*B.L. Fisher et al.*); Toamasina, Amparihibe, 15° 2' S, 49° 34' E, II.–III.2003 (*K.A. Jackson & D. Carpenter*); Toamasina, Analamay, 18.8062 S, 48.3371 E, 1068 m, montane rainforest, 21.III.2004 (*Malagasy ant team*); Toamasina, vic. Andasibe (= Perinet), 950–980 m, 2.–6.II.1977 (*W.L. & D.E. Brown*); Toamasina, F.C. Andriantantely, 18.695 S, 48.8133 E, 530 m, rainforest, 4.–10.XII.1998 (*H.J. Ratsirarson*); Toamasina, Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 15.1883 S, 49.615 E, 470 m, rainforest, 8.–12.III.2003 (*B.L. Fisher, C. Griswold et al.*); Toamasina, Rte d'Anosibe, km 33, 4.–12.IV.1975 (*A. Peyrieras*); Toamasina, Betampona, Ambodiriana, 14.V.1993 (*P. Rabeson*); Toamasina, Reserve Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 17.8867 S, 49.2025 E, 520 m, rainforest, 1.–3.XII.2005 (*B.L. Fisher et al.*); Toamasina, F.C. Didy, 18.1983 S, 48.5783 E, 960 m, rainforest, 16.–23.XII.1998 (*H.J. Ratsirarson*); Toamasina, Mahavelona (Foulpointe), 17.6667 S, 49.5 E, sandy forest & Pandanus marsh, 11.XI.–2.XII.1993 (*A. Pauly*); Toamasina, Parc National Mananara-Nord, 7.1 km 261° Antanambe, 16.455 S, 49.7875 E, 225 m, rainforest, 14.–16.XI.2005 (*B.L. Fisher et al.*); Toamasina, P.N. Mantadia, 18.7917 S, 48.4267 E, 895 m, rainforest, 25.XI.–1.XII.1998 (*H.J. Ratsirarson*); Toamasina, 19 km ESE Maroantsetra, 350 m, rainforest, 22.IV.1989 (*P.S. Ward*); Toamasina, F.C. Sandranantitra, 18.0483 S, 49.0917 E, 450 m, 18.–24.I.1999 (*H.J. Ratsirarson*); Toamasina, Torotorofotsy, 18.8708 S, 48.3474 E, 1070 m, montane rainforest, marsh edge, 24.–29.III.2004 (*Malagasy ant team*); Toamasina, Parc National de Zahamena, Besaky River, 17.7524 S, 48.8532 E, 760 m, rainforest, 22.II.2009 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena, Onibe River, 17.7591 S, 48.8547 E, 780 m, rainforest, 21.–23.II.2009 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena, Sahavorondrano River, 17.7526 S, 48.8573 E, 765 m, rainforest, 23.II.2009 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena, Tetezambatana Forest, near junction of Nosivola and Manakambahiny Rivers, 17.743 S, 48.7294 E, 860 m, rainforest, 18.–19.II.2009 (*B.L. Fisher et al.*); Toliara, Rés. Andohahela, 10 km NW Enakara, 24.5667 S, 46.8167 E, 430 m, rainforest, 22.XI.1992 (*B.L. Fisher*); Toliara, Rés. Andohahela, 11 km NW Enakara, 24.5667 S, 46.8333 E, 800 m, rainforest, 17.XI.1992 (*B.L. Fisher*); Toliara, Res. Andohahela, 6 km SSW Eminiminy, 24° 44' S, 46° 48' E, 330 m, wet forest, 4.II.1993 (*G.D. Alpert et al.*); Toliara, Res. Andohahela, 6 km SSW Eminiminy, 24° 44' S, 46° 48' E, 330 m, rainforest, 4.II.1993 (*P.S. Ward*); Toliara, Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 24.7585 S, 46.8537 E, 275 m, rainforest,22.–24.XI.2006 (*B.L. Fisher et al.*); Toliara, Forêt Ivohibe 55.0 km N Tolagnaro, 24.569 S, 47.204 E, 200 m, rainforest, 2.–4.XII.2006 (*B.L. Fisher et al.*); Toliara, Forêt Ivohibe 55.6 km N Tolagnaro, 24.5617 S, 47.2002 E, 650 m, rainforest, 4.XII.2006 (*B.L. Fisher et al.*).

Tetramorium elf **Hita Garcia & Fisher sp. n.**
(Figs. 12, 56, 58, 62, 63, 87, 88, 89, 141)

Holotype worker, MADAGASCAR, Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, sifted litter (leaf mold, rotten wood), collection code BLF08872, 15.–18.XI.2003 (*B.L. Fisher et al.*) (CASC: CASENT0045788). Paratypes, one worker with same data as holotype (CASC: CASENT0045787); one worker with same data as holotype except sampled from yellow pan trap and collection code BLF08873 (CASC: CASENT0048893); and one worker from Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, ground foragers, collection code BLF09077, 17.XI.2003 (*B.L. Fisher*) (CASC: CASENT0487782).



FIGURES 87–89. *T. elf*, holotype (CASENT0045788). **87.** Body in profile. **88.** Body in dorsal view. **89.** Head in full-face view.

Diagnosis

Tetramorium elf is easily separable from the remainder of the species group due to the following combination of characters: propodeal spines extremely long (PSLI 59–64); petiolar node around 1.2 times higher than long (LPeI 80–83); posterodorsal corner of petiole not strongly protruding posteriorly; mandibles unsculptured, smooth, and shiny; body of yellowish colour.

Description

HL 0.97–1.13 (1.07); HW 0.92–1.06 (1.02); SL 0.76–0.84 (0.81); EL 0.16–0.19 (0.18); PH 0.51–0.65 (0.55); PW 0.68–0.76 (0.73); WL 1.29–1.41 (1.36); PSL 0.59–0.70 (0.66); PTL 0.33–0.37 (0.35); PTH 0.40–0.45 (0.42); PTW 0.29–0.35 (0.32); PPL 0.33–0.38 (0.37); PPH 0.39–0.46 (0.42); PPW 0.35–0.41 (0.38); CI 92–96 (95); SI 78–83 (80); OI 17–18 (18); DMI 53–54 (54); LMI 38–46 (40); PSLI 59–64 (62); PeNI 43–45 (44); LPeI 80–83 (82); DPeI 88–96 (92); PpNI 51–54 (52); LPpI 84–93 (88); DPpI 100–108 (104); PPI 117–122 (119) (ten measured).

Head longer than wider (CI 95–96). Anterior clypeal margin medially impressed. Posterior head margin only weakly concave. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively short, not reaching posterior head margin (SI 78–83). Eyes small (OI 17–18). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–46). Propodeal spines extremely long, spinose, and acute (PSLI 59–64); propodeal lobes short, triangular, and blunt. Petiolar node in profile rectangular nodiform with comparatively rounded angles, around 1.2 times higher than long (LPeI 80–83), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum straight to weakly convex; node in dorsal view around 1.1 times longer than wide (DPeI 88–96). Postpetiole in profile subglobular, approximately 1.1 to 1.2 times higher than long (LPpI 84–93); in dorsal view as wide as long to weakly wider than long (DPpI 100–108). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view approximately 1.2 times wider than petiolar node (PPI 117–122). Mandibles unsculptured, smooth, and shining; clypeus with longitudinally rugulose, usually with three rugulae, median rugula better developed than lateral rugulae; cephalic dorsum between frontal carinae with eight to ten longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, rugae never with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose without cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae with weak, superficial punctate or rugulose sculpture only. Waist segments with weak to moderate rugulose sculpture, especially weakly developed laterally. Ground sculpture everywhere on body faint to absent. First gastral tergite unsculptured, smooth, and shining. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. First gastral tergite without appressed pubescence. Anterior edges of antennal scapes with subdecumbent to erect standing hairs. Body of uniform yellowish colour.

Notes

Tetramorium elf was collected from rainforests in Makirovana, Marojejy, Antalaha, and Ambalagoavy at elevations from 625 to 900 m. Despite being known from four localities, the available material consists of just 12 specimens, making *T. elf* a relatively rarely sampled species. The microhabitat of these ants is not clear since the specimens were collected from the ground, leaf litter, and malaise or pan traps.

The new species is highly conspicuous and not easily confused with another member of the complex. The small eyes (OI 17–18), extremely long propodeal spines (PSLI 59–64), smooth and shiny mandibles, and the distinct yellowish colouration are quite unique in the complex and group. Nevertheless, *T. elf* seems to be morphologically near to *T. electrum* and *T. isoelectrum*. All three share the small eyes (OI 16–19), the enormously developed propodeal spines (PSLI 46–64), usually higher than 50), and relatively small and blunted propodeal lobes. The conspicuous yellowish body colour, longer antennal scapes (SI 78–83), and a lower petiolar node (LPeI 80–83), however, separate *T. elf* from the very dark brown to black *T. electrum* (SI 67–74; LPeI 64–74). In addition, the likewise very darkly coloured *T. isoelectrum* has strongly sculptured mandibles, which contrasts with the unsculptured mandibles of *T. elf*.

Etymology

The new species is named after the "supernatural beings" from Old Norse and Old English myths. The species epithet is a noun in apposition, and thus invariant.

Material examined

MADAGASCAR: Antsiranana, 4 km SW of Antalaha, 31.I.1990 (*G.D. Alpert*); Antsiranana, Makirovana forest, 14.16666 S, 49.95 E, 715 m, rainforest, 30.IV.2011 (*B.L. Fisher et al.*); Antsiranana, Makirovana forest, 14.16506 S, 49.9477 E, 900 m, rainforest, 30.IV.–2.V.2011 (*B.L. Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, 15.–18.XI.2003 (*B.L. Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, 17.XI.2003 (*B.L. Fisher*); Fianarantsoa, Foret d'Ambalagoavy Nord, Ikongo, Ambatombe, 21.8275 S, 47.33889 E, 625 m, 1.XII.2000 (*R. Harin'Hala & M.E. Irwin*).

Tetramorium isectum Bolton, 1979

(Figs. 52, 90, 91, 92, 141)

Tetramorium isectum Bolton, 1979: 145. Holotype worker, MADAGASCAR, Beforona, 500 m, forest humus and litter, IX.1974 (*A. Peyrieras*) (MCZ: CASENT0172829) [examined].

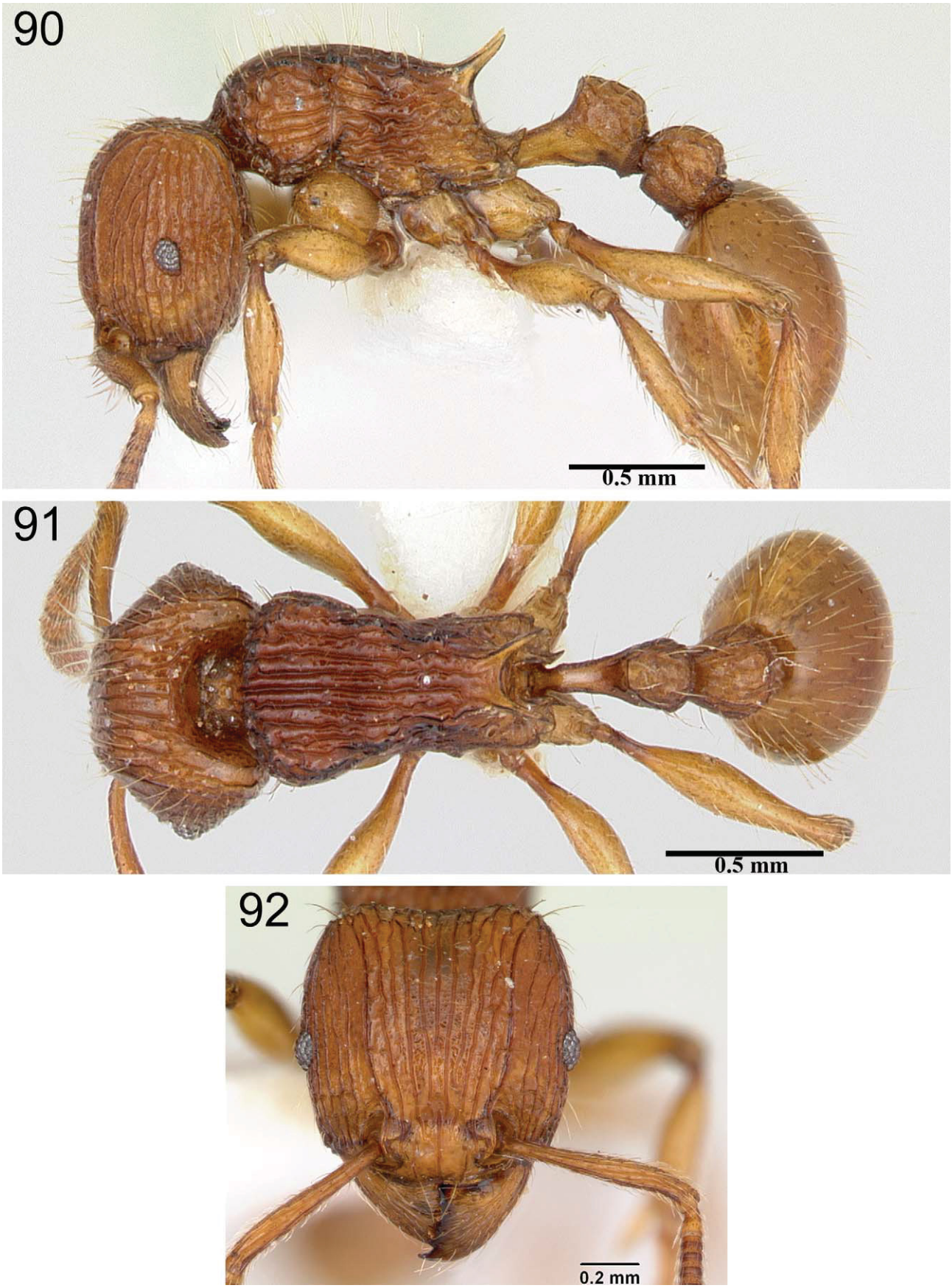
Diagnosis

Within the *T. andrei* complex *T. isectum* is distinguishable by the following characters: very small eyes (OI 15–16); long propodeal spines (PSLI 28–33); petiolar node with the anterodorsal margin slightly situated higher and more angular than the posterodorsal margin; posterodorsal corner of petiole not strongly protruding posteriorly; body of uniform bright orange colour.

Description

HL 0.90–1.10 (0.96); HW 0.85–1.50 (0.93); SL 0.65–0.83 (0.72); EL 0.14–0.18 (0.15); PH 0.42–0.54 (0.47); PW 0.58–0.76 (0.68); WL 1.08–1.39 (1.17); PSL 0.26–0.36 (0.29); PTL 0.25–0.34 (0.28); PTH 0.33–0.40 (0.35); PTW 0.24–0.29 (0.26); PPL 0.27–0.35 (0.31); PPH 0.31–0.39 (0.34); PPW 0.32–0.40 (0.34); CI 94–99 (97); SI 74–79 (77); OI 15–16 (16); DMI 54–60 (58); LMI 39–42 (40); PSLI 28–33 (30); PeNI 36–42 (38); LPeI 71–85 (81); DPeI 86–98 (92); PpNI 49–54 (50); LPpI 82–97 (91); DPpI 103–120 (111); PPI 128–136 (132) (12 measured).

Head usually weakly longer than wide (CI 94–99). Posterior head margin concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes short, not reaching posterior head margin (SI 74–79). Eyes very small (OI 15–16). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 39–42). Propodeal spines long, spinose, and acute (PSLI 28–33); propodeal lobes short, triangular to elongate-triangular, and acute. Petiolar node in profile rectangular nodiform, around 1.2 to 1.4 times higher than long (LPeI 71–85), anterior and posterior faces approximately parallel, anterodorsal margin situated weakly higher and more angulate than posterodorsal margin, dorsum tapering weakly backwards posteriorly; node in dorsal view between 1.0 to 1.2 times longer than wide (DPeI 86–98). Postpetiole in profile globular, approximately 1.0 to 1.2 times higher than long (LPpI 82–97); in dorsal view between 1.0 and 1.2 times wider than long (DPpI 103–120). Postpetiole in profile appearing approximately as voluminous as petiolar node, in dorsal view approximately 1.3 to 1.4 times wider than petiolar node (PPI 128–136). Mandibles distinctly longitudinally rugose; clypeus generally with three distinct longitudinal rugae/rugulae, sometimes with few more but much weaker rugulae present, and very rarely clypeus with irregular rugulation; cephalic dorsum between frontal carinae with 8 to 11 longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, rugae very rarely with cross-meshes; lateral and ventral head longitudinally rugose with very few cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae unsculptured, smooth, and shining. Waist segments irregularly rugulose with distinct punctate ground sculpture, laterally ground sculpture better developed and rugulae weaker. First gastral tergite unsculptured, smooth, and shining. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with decumbent to suberect standing hairs. Body colour bright yellow to orange.



FIGURES 90–92. *T. isectum*, holotype (CASENT0172829). **90.** Body in profile. **91.** Body in dorsal view. **92.** Head in full-face view.

Notes

Prior to our study *T. isectum* was only known from the holotype from Beforona. Fortunately, we had more material available because the species has been collected several times since the original description of Bolton (1979). *Tetramoirum isectum* does not seem to be as rare as might be expected from the original description. We were able to examine material from a number of localities, although the species is admittedly never very common or abundant. *Tetramorium isectum* is found in a strip in eastern Madagascar, which ranges from central-eastern to northeastern Madagascar. The southernmost localities are Ambatovy, Andasibe-Mantadia, and Sahafina, and the northernmost are Montagne d'Anjanaharibe and Amparihibe. The species prefers rainforests and montane rainforests at elevations of 125 to 1040 m, and was mostly collected from leaf litter.

Tetramorium isectum is morphologically fairly close to *T. andrei*, and during this revision we considered the synonymisation of the first under the latter. Both differ mainly in eye size, which is very small in *T. isectum* (OI 15–16) versus small to moderately large in *T. andrei* (OI 19–25), but there a few more supporting characters found in both species, although not consistently. All specimens of *T. isectum* have, in addition to very small eyes, a petiolar node shape with the anterodorsal margin higher and sharper than the posterodorsal with a dorsum that tapers weakly posteriorly, as well as a bright orange body colour. However, within the vast *T. andrei* material available, there are specimens with a node shape like the one of *T. isectum*, although these are mainly restricted to northwestern Madagascar where *T. isectum* does not occur. Many specimens of *T. andrei* are also bright orange in colour. Nevertheless, *T. isectum* was found to live in sympatry with *T. andrei* throughout most of its distribution range, and remained remarkably recognisable. The diagnostic characters of *T. isectum* provided above are very consistent throughout all the material studied, and no intermediate forms seem to exist. With these facts in mind, we keep *T. isectum* a separate though relatively uncommon species which co-occurs regularly with the much more common and abundant *T. andrei*.

Apart from the similarities with *T. andrei* mentioned above, *T. isectum* is easily recognisable within the species complex. The very small eyes (OI 15–16) are very conspicuous with the caveat that *T. electrum*, *T. elf*, *T. isoelectrum*, and *T. nify* also have generally smaller eyes (OI 16–19). However, *T. electrum*, *T. elf*, and *T. isoelectrum* have very long to extremely long propodeal spines (PSLI 46–64), whereas the spines of *T. isectum* are much shorter (PSLI 28–35). *Tetramorium nify* is also unlikely to be misidentified with *T. isectum* since the latter is bright orange in colour and the former is very dark brown to black in colour. In addition, they have fairly differently shaped petiolar nodes. The node of *T. nify* has antero- and posterodorsal margins at the same height and is only faintly higher than long (LPeI 91–100), whereas in *T. isectum* the anterodorsal margin is usually weakly higher and the node is between 1.2 to 1.4 times higher than long (LPeI 71–85). The remaining species, T. ala, *T. andohahela*, and *T. voasary*, have much larger eyes (OI 20–24) and differently shaped petiolar nodes, and are thus not easy to confuse with *T. isectum*.

Material examined

MADAGASCAR: Mahajanga, Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, 16.2832 S, 48.8144 E, 865 m, transition humid forest, 6.–8.XII.2007 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato river, 16.8175 S, 49.295 E, 360 m, rainforest, 25.–27.II.2010 (*B.L. Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8496 S, 48.2947 E, 1010 m, montane rainforest, 3.–6.III.2007 (*B.L. Fisher et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8477 S, 48.2947 E, 1000 m, montane rainforest, 5.–8.III.2007 (*B.L. Fisher et al.*); Toamasina, Res. Ambodiriana, 4.8 km 306° Manompana, along Manompana river, 16.6723 S, 49.7012 E, 125 m, rainforest, 18.XI.2005 (*B.L. Fisher et al.*); Toamasina, Amparihibe, 15° 2' S, 49° 34' E, II.–III.2003 (*K.A. Jackson & D. Carpenter*); Toamasina, Station forestière Analamazaotra, Analamazaotra 1.3 km S Andasibe, 18.3847 S, 48.4127 E, 980 m, montane rainforest, 11.–13.XII.2007 (*B.L. Fisher et al.*); Toamasina, Parc National d´Andasibe-Mantadia, Forêt de Mantadia, 25.7 km 248° Moramanga, 18.814 S, 48.4303 E, 1040 m, rainforest, 14.VII.2006 (*F.N. Raharimalala & B. Blaimer*); Toamasina, Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 15.1883 S, 49.615 E, 470 m, rainforest, 8.–12.III.2003 (*B.L Fisher, C. Griswold et al.*); Toamasina, Beforona, 500 m, IX.1974 (*A. Peyrieras*); Toamasina, Parc National Mananara-Nord, 7.1 km 261° Antanambe, 16.455 S, 49.7875 E, 225 m, rainforest, 14.XI.2005 (*B.L. Fisher et al.*); Toamasina, Sahafina forest 11.4 km W Brickaville, 18.8144 S, 48.9621 E, 140 m, rainforest, 13.–14.XII.2007 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena, Onibe River, 17.7591 S, 48.8547 E, 780 m, rainforest, rainforest, 21.–23.II.2009 (*B.L. Fisher et al.*); Toamasina, Parc National de Zahamena,

Tetezambatana forest, near junction of Nosivola and Manakambahiny Rivers, 17.74298 S, 48.72936 E, 860 m, rainforest, 18.–19.II.2009 (*B.L. Fisher et al.*).

Tetramorium isoelectrum Hita Garcia & Fisher sp. n.

(Figs. 59, 64, 65, 93, 94, 95, 141)

Holotype worker, MADAGASCAR, Antsiranana, Betaolana Forest, along Bekona River, 14.52996 S, 49.44039 E, 880 m, rainforest, on low vegetation, collection code BLF22647, 5.III.2009 (*B.L. Fisher et al.*) (CASC: CASENT0152199). Paratype, one worker with same data as holotype except sampled from ground and collection code BLF22648 (CASC: CASENT0152192).

Diagnosis

Tetramorium isoelectrum differs from the remainder of the species group by the following character combination: propodeal spines extremely long (PSLI 58–63); petiolar node around 1.1 to 1.3 times higher than long (LPeI 79–86); posterodorsal corner of petiole not strongly protruding posteriorly; mandibles with distinct longitudinal sculpture; body dark brown to black in colour.

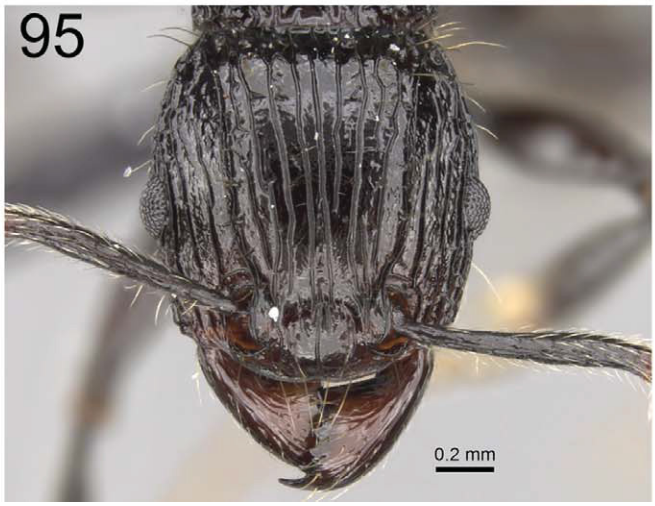
Description

HL 1.09–1.19 (1.16); HW 1.03–1.13 (1.10); SL 0.84–0.94 (0.91); EL 0.19–0.21 (0.20); PH 0.53–0.68 (0.61); PW 0.74–0.84 (0.81); WL 1.36–1.57 (1.50); PSL 0.63–0.75 (0.71); PTL 0.35–0.38 (0.36); PTH 0.44–0.46 (0.45); PTW 0.32–0.34 (0.33); PPL 0.38–0.40 (0.39); PPH 0.44–0.46 (0.45); PPW 0.39–0.41 (0.40); CI 93–96 (95); SI 81–84 (82); OI 17–19 (18); DMI 53–55 (54); LMI 38–45 (40); PSLI 58–63 (61); PeNI 38–46 (41); LPeI 79–86 (81); DPeI 87–93 (90); PpNI 47–54 (49); LPpI 83–91 (87); DPpI 101–105 (103); PPI 118–127 (123) (seven measured).

Head longer than wide (CI 93–96). Posterior head margin weakly to moderately concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively short to moderately long, not reaching posterior head margin (SI 81–84). Eyes small (OI 17–19). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–45). Propodeal spines extremely long, spinose, and acute (PSLI 58–63); propodeal lobes short, triangular, and blunt. Petiolar node in profile rectangular nodiform with comparatively rounded angles, around 1.1 to 1.3 times higher than long (LPeI 79–86), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum straight to weakly convex; node in dorsal view around 1.1 times longer than wide (DPeI 87–93). Postpetiole in profile subglobular, approximately 1.1 to 1.2 times higher than long (LPpI 83–91); in dorsal view feebly wider than long (DPpI 101–105). Postpetiole in profile appearing a bit more voluminous than petiolar node, in dorsal view approximately 1.2 to 1.3 times wider than petiolar node (PPI 118–127). Mandibles distinctly longitudinally rugose; clypeus with four to six longitudinal rugulae, median rugula better developed than lateral rugulae; cephalic dorsum between frontal carinae with eight to ten longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, rugae never with cross-meshes; lateral and ventral head longitudinally rugose with very few cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose, rugae laterally more irregularly arranged. Forecoxae mainly reticulate-punctate with superficial, superimposed rugulae. Waist segments with reticulate-rugose to longitudinally rugose sculpture. Ground sculpture everywhere on body faint to absent. First gastral tergite unsculptured, smooth, and shining. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. First gastral tergite without appressed pubescence. Anterior edges of antennal scapes with subdecumbent to erect standing hairs. Body of uniform very dark brown to black colour.

Notes

Currently, this new species is only known from seven specimens from Betaolana, Befingotra, and Marojejy. All three localities are rainforests found in the north-eastern part of Madagascar at elevations of 450 to 880 m.



FIGURES 93–95. *T. isoelectrum*, holotype (CASENT0152199). **93.** Body in profile. **94.** Body in dorsal view. **95.** Head in full-face view.

Tetramorium isoelectrum is morphologically very close to *T. electrum* and *T. elf*, as outlined in the descriptions of the latter two species. *Tetramorium elf*, however, is yellow in colour and has mandibles that are unsculptured, smooth, and shining, whereas *T. isoelectrum* is very dark brown and has mandibles that are very clearly sculptured. *T. isoelectrum* and *T. electrum* are more difficult to distinguish. Both species are very close in general gestalt and easy to confuse at first glance. Nevertheless, *T. isoelectrum* has a longer head (CI 93–96), longer antennal scapes (SI 81–84), and a longer and lower petiolar node (LPeI 77–86; DPeI 87–97) than *T. electrum* (CI 98–104; SI 67–74; LPeI 64–74; DPeI 100–114). Furthermore, due to its extremely long propodeal spines (PSLI 58–63), *T. isoelectrum* is not likely to be misidentified with the remaining species of the complex.

Etymology

The name of the new species is composed of "iso", which is Old Greek meaning "equal", and "electrum", which is the species epithet of *T. electrum*. *Tetramorium electrum* and *T. isoelectrum* are very similar, and the new species name reflects this. The species epithet is a noun in apposition, and thus invariant.

Material examined

MADAGASCAR: Antsiranana, 6.5 km SSW Befingotra, Rés. Anjanaharibe-Sud, 14.75 S, 49.5 E, 875 m, rainforest, 20.IX.1994 (*B.L. Fisher*); Antsiranana, Betaolana Forest, along Bekona River, 14.52996 S, 49.44039 E, 880 m, rainforest, 5.III.2009 (*B.L. Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14.43667 S, 49.775 E, 450 m, rainforest, 12.–15.XI.2003 (*B.L. Fisher et al.*).

Tetramorium nify Hita Garcia & Fisher sp. n.

(Figs. 61, 68, 69, 96, 97, 98)

Holotype worker, MADAGASCAR, Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.81753 S, 49.29498 E, 360 m, rainforest, ex rotten log, collection code BLF24814, 25.II.2010 (*B.L. Fisher et al.*) (CASC: CASENT0163155). Paratype, one worker with same data as holotype (CASC: CASENT0163345).

Diagnosis

Tetramorium nify can be clearly distinguished from the other species of the *T. andrei* complex by the following character combination: small eyes (OI 16–17); long propodeal spines (PSLI 29–30); posterodorsal corner of petiolar node not strongly protruding posteriorly; body very dark brown to black in colour.

Description

HL 0.83–0.95 (0.87); HW 0.82–0.93 (0.86); SL 0.60–0.66 (0.63); EL 0.14–0.15 (0.14); PH 0.41–0.51 (0.44); PW 0.61–0.72 (0.65); WL 1.02–1.21 (1.08); PSL 0.25–0.28 (0.26); PTL 0.30–0.37 (0.33); PTH 0.32–0.38 (0.35); PTW 0.26–0.31 (0.28); PPL 0.29–0.33 (0.31); PPH 0.32–0.37 (0.34); PPW 0.33–0.38 (0.35); CI 98–100 (99); SI 69–74 (73); OI 16–17 (17); DMI 59–63 (60); LMI 39–42 (41); PSLI 29–30 (30); PeNI 43–44 (43); LPeI 91–100 (96); DPeI 82–88 (84); PpNI 52–54 (53); LPpI 88–91 (90); DPpI 112–116 (113); PPI 121–125 (124) (five measured).

Head weakly longer than wider to as long as wide (CI 98–100). Posterior had margin weakly concave. Anterior clypeal margin weakly medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes moderately developed, but shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively short, not reaching posterior head margin (SI 69–74). Eyes very small (OI 16–17). Mesosomal outline in profile flat, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 39–42). Propodeal spines with very broad base, up-curved, elongate-triangular, and moderately long (PSLI 29–30); propodeal lobes well-developed, triangular and acute. Petiolar node in profile

rectangular nodiform with well-defined angles, around 1.0 to 1.1 times higher than long (LPeI 91–100), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum straight; node in dorsal view approximately 1.2 times longer than wide (DPeI 82–88). Postpetiole in profile globular, approximately 1.1 times higher than long (LPpI 88–91); in dorsal view around 1.1 to 1.2 times wider than long (112–116). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view approximately 1.2 times wider than petiolar node (PPI 121–125). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose, with three to five rugae; cephalic dorsum between frontal carinae with 8 to 11 longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, few rugae interrupted or with cross-meshes; lateral and ventral head longitudinally rugose, rarely with cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae unsculptured. Waist segments strongly irregularly longitudinally rugose. Gaster completely unsculptured, smooth and shining. Ground sculpture generally faint to absent everywhere on body. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. First gastral tergite without appressed pubescence. Anterior edges of antennal scapes with erect, standing hairs. Body uniform dark brown to black in colour.

Notes

Tetramorium nify is only known from five specimens from Ambatovaky, Befingotra, and Isle Saint Marie.

Within the species complex, *T. nify* is another species with fairly small eyes (OI 16–17). The other species with comparatively small eyes are *T. elf, T. electrum, T. isoelectrum,* and *T. isectum*. The first three have very long to extremely long propodeal pines (PSLI 46–64), short and blunted propodeal lobes, and differently shaped petiolar nodes. *Tetramorium isectum* has even smaller eyes (OI 15–16) than *T. nify*, a petiolar node with the anterodorsal margin situated higher than the posterodorsal and the dorsum weakly tapering backwards, and bright orange body colour, whereas *T. nify* is very dark brown to black in colour and has anterodorsal and posterodorsal margins of the petiolar node at about the same height. Disregarding eye size, *T. nify* also cannot be confused with *T. ala*, *T. andohahela*, or *T. voasary. Tetramorium andohahela* has the posterodorsal corner of the petiolar node strongly protruding posteriorly, *T. ala* has the posterior corners of the head weakly angular and marginate, and *T. voasary* has a petiolar node with the anterodorsal and posterodorsal angles fairly rounded. The defining characters of the first two are absent in *T. nify*, and the petiole of the latter has a node with well-defined anterodorsal and posterodorsal angles, which separates it from *T. voasary.*

The last species of the complex, *T. andrei*, is morphologically very close to *T. nify*, and we have treated the material as conspecific for a while during this revision. The only good diagnostic character that divides them is eye size, which is much larger in *T. andrei* (OI 19–25, usually above 20). However, we observed both in sympatry in Ambatovaky and Befingotra and specimens of *T. nify* are easily separable from sympatric *T. andrei* due to their fairly small eyes and a petiolar node with sharper defined antero- and posterodorsal margins. The mesosoma of *T. nify* is also a bit shorter (DMI 59–63) than the one of *T. andrei* (DMI 50–60). As noted in its description, *T. andrei* is a remarkably variable species, which very likely includes several cryptic species. However, especially on the basis of the co-occurrence without intermediate forms, we treat *T. nify* as its own species distinct from *T. andrei*.

Etymology

The species epithet is an arbitrary combination of letters.

Material examined

MADAGASCAR: Antsiranana, Rés. Anjanaharibe-Sud, 6.5 km SSW Befingotra, 14.75 S, 49.5 E, 875 m, rainforest, 18.–22.X.1994 (*B.L. Fisher*); Toamasina, Ile Sainte Marie, Forêt Kalalao, 9.9 km 34° Ambodifotatra, 16.9225 S, 49.88733 E, 100 m, rainforest, 24.–27.XI.2005 (*B.L. Fisher et al.*); Toamasina, Réserve Spéciale Ambatovaky, Sandrangato River, 16.81753 S, 49.29498 E, 360 m, rainforest, 25.II.2010 (*B.L. Fisher et al.*).

FIGURES 96–98. *T. nify*, holotype (CASENT0163155). **96.** Body in profile. **97.** Body in dorsal view. **98.** Head in full-face view.

Tetramorium voasary **Hita Garcia & Fisher sp. n.**
(Figs. 60, 71, 72, 99, 100, 101, 141)

Holotype worker, MADAGASCAR, Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 15.17833 S, 49.635 E, 1100 m, montane rainforest, canopy moss and leaf litter, collection code BLF08213, 12.–16.III.2003 (*B.L. Fisher, C. Griswold et al.*) (CASC: CASENT0247162). Paratypes, 11 workers with same data as holotype (CASC: CASENT0497903; CASENT0497904; CASENT0497905; CASENT0497906); and one worker with same data as holotype except sampled from beating low vegetation and collection code BLF08151 (CASC: CASENT0489080).

Diagnosis
Tetramorium voasary can be clearly distinguished from the remainder of the species complex by the following character combination: eyes moderately sized (OI 21–24); propodeal spines long to very long (PSLI 35–39); petiolar node rectangular nodiform but with relatively rounded anterodorsal and posterodorsal angles; posterodorsal corner of petiolar node not strongly protruding posteriorly; postpetiole in dorsal view usually slightly longer than wide, rarely as wide as long or longer than wide (DPpI 95–101); body uniform bright orange in colour.

Description
HL 0.94–1.23 (1.07); HW 0.87–1.15 (0.98); SL 0.70–0.99 (0.81); EL 0.18–0.27 (0.23); PH 0.49–0.59 (0.53); PW 0.69–0.80 (0.73); WL 1.20–1.49 (1.36); PSL 0.36–0.46 (0.39); PTL 0.32–0.36 (0.35); PTH 0.37–0.42 (0.40); PTW 0.29–0.34 (0.31); PPL 0.34–0.42 (0.38); PPH 0.36–0.43 (0.39); PPW 0.34–0.41 (0.38); CI 88–93 (92); SI 80–89 (82); OI 21–24 (23); DMI 52–58 (54); LMI 38–42 (39); PSLI 35–39 (37); PeNI 41–47 (43); LPeI 85–93 (89); DPeI 85–94 (90); PpNI 48–55 (52); LPpI 90–104 (97); DPpI 95–101 (98); PPI 113–125 (120) (ten measured).

Head distinctly longer than wider (CI 88–93). Posterior head margin weakly concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively moderately long, not reaching posterior head margin (SI 80–89). Eyes small to moderately sized (OI 21–24). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–42). Propodeal spines long to very long, spinose, and acute (PSLI 35–39); propodeal lobes short, triangular, and rounded, rarely acute. Petiolar node in profile rectangular nodiform with fairly rounded margins, around 1.1 to 1.2 times higher than long (LPeI 85–93), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum weakly to moderately convex; node in dorsal view around 1.1 to 1.2 times longer than wide (DPeI 85–94). Postpetiole in profile globular, ranging from weakly longer than high to 1.1 times higher than long (LPpI 90–104); in dorsal view ranging from weakly longer than wide to feebly wider than long (DPpI 95–101). Postpetiole in profile appearing approximately as voluminous as petiolar node, in dorsal view approximately 1.1 to 1.3 times wider than petiolar node (PPI 113–125). Mandibles distinctly longitudinally rugose, sometimes weakly so; sculpture on clypeus variable, often longitudinally rugulose with three to five rugulae, sometimes more irregularly rugulose; cephalic dorsum between frontal carinae with seven to ten longitudinal rugae, rugae often broken or with cross-meshes; lateral and ventral head mostly reticulate-rugose. Mesosoma laterally and dorsally mainly longitudinally rugose. Forecoxae usually completely unsculptured, smooth, and shiny, sometimes with partial superficial sculpture. Waist segments rugulose, usually longitudinally so. Generally ground sculpture everywhere on body faint to absent. First gastral tergite unsculptured, smooth, and shining. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with suberect to erect standing hairs. Body of bright orange to light orange brown colour.

Notes
This new species is distributed in the rainforests and montane rainforests of eastern Madagascar from Befotaka-Midongo in the south to Makirovana in the northeast. The distribution range is comparatively large, but localities where *T. voasary* was encountered are often widely separated. Despite being known from approximately ten localities, *T. voasary* was collected relatively rarely with less than 25 specimens in total. One explanation might be that the species lives and forages in vegetation; it was mostly collected from lower vegetation, and only rarely from the ground or leaf litter.

FIGURES 99–101. *T. voasary*, holotype (CASENT0247162). **99.** Body in profile. **100.** Body in dorsal view. **101.** Head in full-face view.

Due to its well-developed eyes (OI 21–24), *T. voasary* is unlikely to be mistaken for *T. electrum*, *T. elf*, *T. isectum*, *T. isoelectrum*, or *T. nify* since they all have much smaller eyes (OI 15–19). The remaining three species, *T. ala*, *T. andohahela*, and *T. andrei*, all have a petiolar node with well-defined antero- and posterodorsal margins while the node of *T. voasary* has fairly rounded margins. This character is shared with *T. elf* and *T. isoelectrum*, although they are not likely to be confused with *T. voasary*. Apart from the small eyes mentioned above, the first two also have extremely long propodeal spines (PSLI 58–64) that contrast with the shorter spines of *T. voasary* (PSLI 35–39).

Etymology
The species epithet is an arbitrary combination of letters.

Material examined
MADAGASCAR: Antsiranana, Makirovana forest, 14.1707 S, 49.9541 E, 415 m, rainforest, 28.IV.2011 (*B.L. Fisher et al.*); Fianarantsoa, Foret d'Ambalagoavy Nord, Ikongo, Ambatombe, 21.8275 S, 47.3389 E, 625 m, 1.XII.2000 (*R. Harin'Hala & M.E. Irwin*); Fianarantsoa, Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango,23.83517 S, 46.96367 E, 940 m, rainforest, 13.–15.XI.2006 (*B.L. Fisher et al.*); Fianarantsoa, Réserve Speciale Manombo 24.5 km 228° Farafangana, 23.0158 S, 47.719 E, 30 m, rainforest, 22.IV.2006 (*B.L. Fisher et al.*); Fianarantsoa, Ranomafana, 21.25 S, 47.3667 E, in forest along riverbank, 1.III.1994 (*A. Pauly*); Fianarantsoa, Ranomafana National Park, Talatakely, 30.X.–20.XI.1998 (*V.F. Lee & K.J. Ribardo*); Fianarantsoa, Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 21.29 S, 47.4333 E, 1100 m, montane rainforest, 27.–31.III.2003 (*B.L. Fisher, C. Griswold et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.8496 S, 48.2947 E, 1010 m, 3.–6.III.2007 (*B.L. Fisher et al.*); Toamasina, Amparihibe, 15° 2' S, 49° 34' E, II.–III.2003 (*K.A. Jackson & D. Carpenter*); Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 15.1783 S, 49.635 E, 1100 m, montane rainforest, 12.–16.III.2003 (*B.L. Fisher, C. Griswold et al.*); Toamasina, Torotorofotsy, 18.8708 S, 48.3474 E, 1070 m, montane rainforest, marsh edge, 24.III.2004 (*Malagasy ant team*).

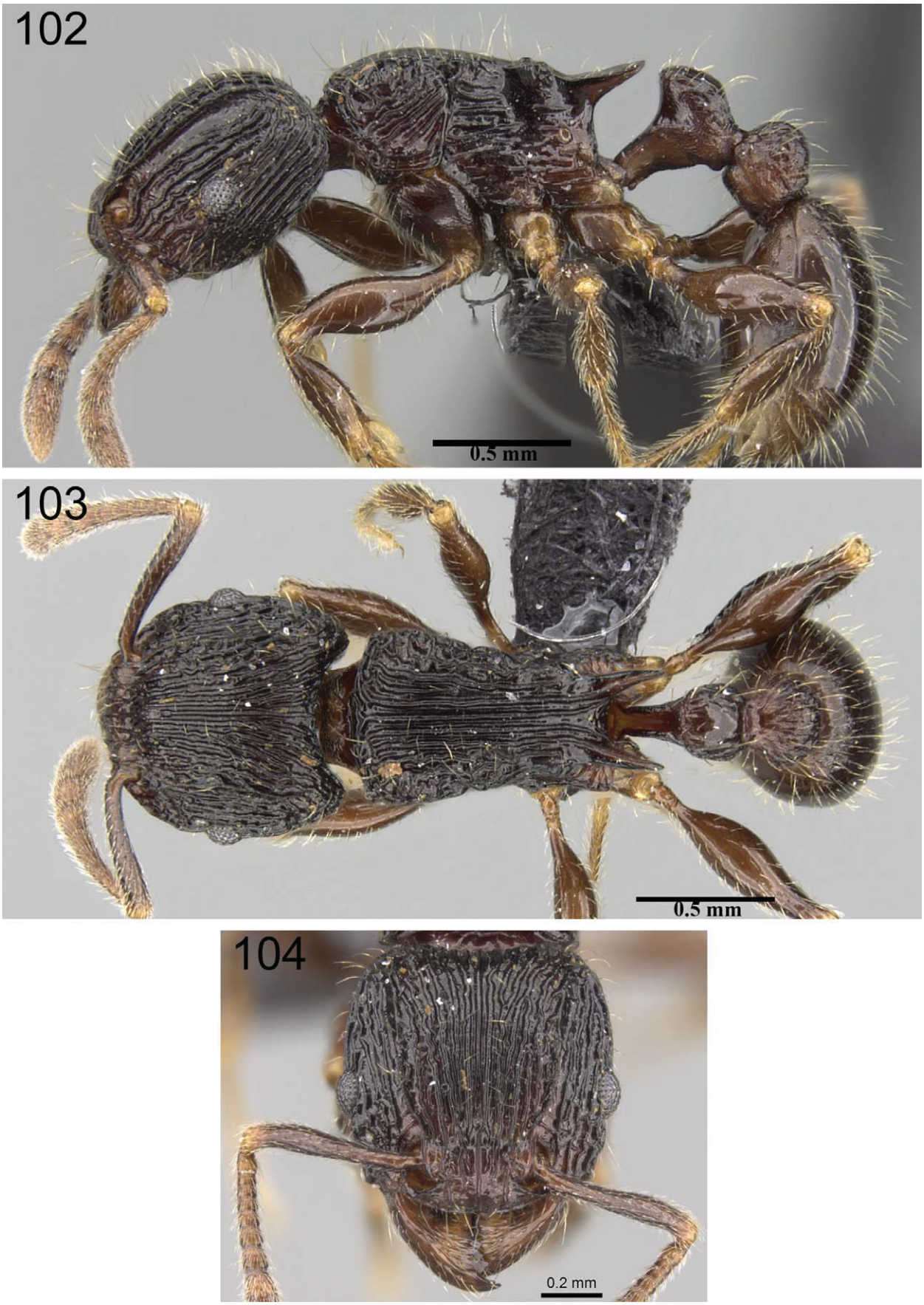
Tetramorium jedi species complex

The *T. jedi* complex is relatively small with just the three species *T. avaratra*, *T. jedi*, and *T. pleganon*. It is characterized by the absence of sculpture on the forecoxae and the presence of reticulate-punctate sculpture on the first gastral tergite.

Tetramorium jedi does not seem to be morphologically close to the other two species of the complex, and they were grouped together on the basis of the reticulate-punctate sculpture on the first gastral tergite present in all three, even though the development of the sculpture from *T. jedi* to *T. avaratra* and *T. pleganon* is fairly different. The latter two, as mentioned above, may not be closely associated with any other *T. tortuosum* group members. *Tetramorium jedi*, however, might be distantly related to *T. andrei* and allies since the main separating character is the conspicuous sculpture on the first gastral tergite present in *T. jedi* but absent in the *T. andrei* complex.

Tetramorium avaratra Hita Garcia & Fisher sp. n.
(Figs. 46, 47, 49, 102, 103, 104, 141)

Holotype worker, MADAGASCAR, Antsiranana, Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, 12.90889 S, 49.10983 E, 80 m, tropical dry forest, sifted litter (leaf mold, rotten wood), collection code BLF02858, 10.–16.II.2001 (*B.L. Fisher, C. Griswold et al.*) (CASC: CASENT0445167). Paratypes, 15 workers with same data as holotype (BMNH: CASENT0443679; CASC: CASENT0439463; CASENT0443689; CASENT0445147; CASENT0445161; CASENT0445174; CASENT0448424; CASENT0448440; CASENT0448557; CASENT0448579; CASENT0448643; CASENT0448665; MCZ: CASENT0443659; MHNG: CASENT0448417; NHMB: CASENT0448568).



FIGURES 102–104. *T. avaratra*, holotype (CASENT0445167). **102.** Body in profile. **103.** Body in dorsal view. **104.** Head in full-face view.

Diagnosis

Tetramorium avaratra is easily recognisable within the *T. jedi* complex due to the following character combination: propodeal spines long (PSLI 27–34 without the Nosy Be specimens, and PSLI 27–37 with the Nosy Be material); petiolar node in dorsal view between 1.2 to 1.4 times wider than long (DPeI 126–137); dorsum of petiolar node only weakly rugose; base of first gastral tergite with superficial, fine, reticulate-punctate sculpture.

Description

HL 0.81–0.94 (0.88); HW 0.78–0.94 (0.87); SL 0.56–0.65 (0.60); EL 0.15–0.18 (0.17); PH 0.41–0.48 (0.45); PW 0.59–0.71 (0.65); WL 1.02–1.20 (1.12); PSL 0.24–0.33 (0.28); PTL 0.19–0.24 (0.22); PTH 0.33–0.40 (0.37); PTW 0.26–0.31 (0.29); PPL 0.23–0.30 (0.27); PPH 0.29–0.37 (0.34); PPW 0.30–0.38 (0.35); CI 97–101 (99); SI 66–72 (69); OI 18–20 (19); DMI 56–60 (57); LMI 38–41 (40); PSLI 27–37 (32); PeNI 43–46 (44); LPeI 54–66 (60); DPeI 126–137 (130); PpNI 50–56 (54); LPpI 74–85 (79); DPpI 124–137 (130); PPI 116–125 (120) (15 measured).

Head approximately as long as wide (CI 97–101); posterior head margin moderately concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, moderately deep, and broad, without defined ventral margins. Antennal scapes very short, not reaching posterior head margin (SI 66–72). Eyes short (OI 18–20). Mesosomal outline in profile flat to weakly convex, strongly marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–41). Propodeal spines long, spinose and acute (PSLI 27–37); propodeal lobes short, triangular, and moderately acute. Petiolar node in profile rectangular nodiform, approximately 1.5 to 1.8 times higher than long (LPeI 54–66), anterior and posterior faces approximately parallel, anterodorsal margin situated higher than posterodorsal, dorsum noticeably tapering backwards posteriorly; node in dorsal view approximately 1.2 to 1.4 times wider than long (DPeI 126–137). Postpetiole in profile rounded, approximately 1.2 to 1.4 times higher than long (LPpI 74–85); in dorsal view around 1.2 to 1.4 times wider than long (DPpI 124–137). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view 1.1 to 1.3 times wider than petiolar node (PPI 116–125). Mandibles finely to strongly striate; clypeus longitudinally rugose, with four to eight rugae, median ruga always present, well-developed and distinct, remaining rugae variably developed, usually weaker and sometimes irregularly arranged; cephalic dorsum between frontal carinae with 11 to 13 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted and none with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose with very few cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose, lateral mesosoma sometimes weaker sculptured than dorsum. Forecoxae generally unsculptured, smooth, and shining, at most with superficial sculpture. Ground sculpture on head and mesosoma generally faint to absent. Waist segments weakly to moderately rugose, sculpture on petiolar node weaker than on postpetiole; both waist segments with conspicuous reticulate-punctate ground sculpture. First gastral tergite with superficial, fine reticulate-punctate sculpture, generally restricted to basal third of the tergite, in several specimens sculpture fairly reduced, but always present. All dorsal surfaces of body with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with decumbent to suberect hairs. Body of uniform brown to dark brown colour, appendages often of lighter colour.

Notes

This new species is restricted in its distribution to several localities in the northern tip of Madagascar and Nosy Be. Interestingly, there is no material known from the area between the population on Nosy Be and the other localities from Andavakoera, Ankarana, Bekaraoka, Ampondrabe, and Analamerana. *Tetramorium avaratra* appears to have comparatively flexible habitat requirements, having been found in rainforests, tropical dry forests, and on tsingy. Also, *T. avaratra* appears to be a ground-active species sampled mainly from leaf litter, and seems restricted to low elevations of 30 to 425 m.

Tetramorium avaratra shows variation in two important morphological characters. First, the propodeal spines of *T. avaratra* are usually long, but relatively short for the *T. tortuosum* group, with a PSLI of 27–34 with a mean value of 31. The few specimens known from the island of Nosy Be, however, have significantly longer spines (PSLI 37–39). This is the only difference observed, and we consider it to be geographic variation since, as mentioned above, the Nosy Be population is fairly widely separated from the other *T. avaratra* populations. The second interesting character, which is variable, is the sculpture on the first gastral tergite. Generally, the reticulate-

punctate ground sculpture is well-developed on the basal third and fairly conspicuous. Nevertheless, in some specimens from Ankarana and Andavakoera, this character is often weakly developed, but still always present and visible.

Within the complex, *T. avaratra* cannot be mistaken with *T. jedi*. The latter species has much more pronounced sculpture on the whole first gastral tergite, which is densely and strongly reticulate-punctate, while the sculpture in *T. avaratra* is only superficial, much less developed, and restricted to the basal third of the first gastral tergite. In addition, both differ in the shape of the petiolar node since it is distinctly longer than wide in *T. jedi* (DPeI 79–85), whereas it is wider than long in *T. avaratra* (DPeI 126–137). The third species in the *T. jedi* complex, *T. pleganon*, is morphologically much closer to *T. avaratra*. *Tetramorium pleganon* differs from *T. avaratra* in several aspects, although some are not obvious at first glance. The propodeal spines are generally much longer in *T. pleganon* (PSLI 37–44) than in *T. avaratra* (PSLI 27–34 without the Nosy Be specimens, PSLI 27–37 with the Nosy Be material). Additionally, the petiolar node dorsum is wider and higher in *T. avaratra* (DPeI 126–137; LPeI 54–66) than in *T. pleganon* (DPeI 111–118; LPeI 63–73. Apart from these differences, both species differ also in the development of sculpture on the waist segments and the first gastral tergite, which is generally less well-developed in *T. avaratra* than in *T. pleganon*. This is especially visible on the dorsum of the petiolar node, which is always strongly rugose in *T. pleganon* but much less rugose in *T. avaratra*, where it is partly smooth. The distribution ranges of both species overlap. Indeed, *T. pleganon* and *T. avaratra* are found in sympatry in Ankarana while retaining their species-characteristics, providing additional evidence for their heterospecificity.

As already mentioned above, it is possible that *T. avaratra* and *T. pleganon* are not members of the *T. tortuosum* group. The petiolar nodes of both are wider than long in dorsal view (DPeI 111–137) while all other *T. tortuosum* group species have petiolar node shapes that range from distinctly longer than wide to weakly wider than long (DPeI 72–114, usually below 100). Also, the general morphology of *T. avaratra* and *T. pleganon*, in particular the shape of the petiolar node and strong margination, is very close to some species from the *T. dysalum* species group, especially *T. dysalum*. However, no member of the *T. dysalum* group has a sculptured first gastral tergite, which clearly distinguishes *T. avaratra* and *T. pleganon* from that group despite the strong general similarity with *T. dysalum*. The latter species also has completely unsculptured mandibles, whereas the mandibles of *T. avaratra* and *T. pleganon* are always sculptured, even though sometimes only finely so. At present, we consider these two species best placed within the *T. tortuosum* group, but cannot discount that they might be more closely related to another species group or represent a lineage parallel to other Malagasy species groups.

Etymology

The species epithet is an arbitrary combination of letters.

Material examined

MADAGASCAR: Antsiranana, Forêt d'Ampondrabe, 26.3km 10° NNE Daraina, 12.97 S, 49.7 E, 175 m, tropical dry forest, 10.XII.2003 (*B.L. Fisher*); Antsiranana, Rés. Analamerana, 28.4 km 99° Anivorano-Nord, 12.74667 S, 49.49483 E, 60 m, tropical dry forest, 5.XII.2004 (*B.L. Fisher*); Antsiranana, Forêt d' Andavakoera, 21.4 km 75° ENE Ambilobe, 13.11833 S, 49.23 E, 425 m, rainforest 15.XII.2003 (*B.L. Fisher*); Antsiranana, Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, 12.90889 S, 49.10983 E, 80 m, tropical dry forest, 10.–16.II.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Réserve Spéciale de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, 12.86361 S, 49.22583 E, 210 m, tropical dry forest, 16.–21.II.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Forêt de Bekaraoka, 6.8 km 60° ENE Daraina, 13.16667 S, 49.71 E, 150 m, tropical dry forest, 7.XII.2003 (*B.L. Fisher*); Antsiranana, Nosy Be, Réserve Naturelle Intégrale de Lokobe, 6.3 km 112° ESE Hellville, 13.41933 S, 48.33117 E, 30 m, rainforest, 19.–24.III.2001 (*B.L. Fisher, C. Griswold et al.*).

***Tetramorium jedi* Hita Garcia & Fisher sp. n.**

(Figs. 29, 33, 44, 45, 105, 106, 107, 142)

Holotype worker, MADAGASCAR, Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, 13.26333 S, 49.60333 E, 800 m, rainforest, 3.XII.2003 (*B.L. Fisher*) (CASC: CASENT0043578). Paratypes, one worker with

same data as holotype (CASC: CASENT0043685); and nine workers from Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, 13.26333 S, 49.60333 E, 725 m, rainforest, ex root mat, ground layer, collection code BLF09691, 4.XII.2003 (*B.L. Fisher*) (CASC: CASENT0077773, CASENT0077774, CASENT0077775).

Diagnosis

Tetramorium jedi is easily distinguished from the remainder of the *T. jedi* species complex by the following characters: petiolar node in dorsal view distinctly longer than wide (DPeI 79–85); entire first gastral tergite conspicuously reticulate-punctate.

Description

HL 0.92–1.03 (0.99); HW 0.87–0.97 (0.93); SL 0.64–0.75 (0.71); EL 0.17–0.20 (0.18); PH 0.45–0.54 (0.49); PW 0.65–0.72 (0.70); WL 1.14–1.30 (1.24); PSL 0.34–0.41 (0.37); PTL 0.29–0.34 (0.32); PTH 0.34–0.40 (0.38); PTW 0.24–0.29 (0.27); PPL 0.30–0.34 (0.31); PPH 0.34–0.41 (0.39); PPW 0.36–0.40 (0.38); CI 92–95 (93); SI 74–79 (77); OI 18–22 (20); DMI 54–58 (56); LMI 38–42 (39); PSLI 35–40 (37); PeNI 37–41 (38); LPeI 80–88 (84); DPeI 79–85 (83); PpNI 53–57 (54); LPpI 76–87 (81); DPpI 116–126 (121); PPI 138–148 (142) (12 measured).

Head distinctly longer than wider (CI 92–95); posterior head margin moderately concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly to moderately developed, shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively short, not reaching posterior head margin (SI 74–79). Eyes small to moderate in size (OI 18–22). Mesosomal outline in profile weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–42). Propodeal spines long, spinose, and acute (PSLI 35–40); propodeal lobes short, triangular and acute. Petiolar node in profile rectangular nodiform, around 1.1 to 1.3 times higher than long (LPeI 80–88), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum straight; node in dorsal view around 1.2 to 1.3 times longer than wide (DPeI 79–85). Postpetiole in profile subglobular, approximately 1.1 to 1.3 times higher than long (LPpI 76–87); in dorsal view around 1.1 to 1.3 times wider than long (DPpI 116–126). Postpetiole in profile appearing as voluminous as petiolar node, in dorsal view approximately 1.3 to 1.5 times wider than petiolar node (PPI 138–148). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose, with three to five rugae/rugulae, median ruga well-developed, lateral rugae/rugulae often weak and broken; cephalic dorsum between frontal carinae with 8 to 11 longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, few rugae interrupted or with cross-meshes; lateral and ventral head longitudinally rugose to reticulate-rugose. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae with weak, superficial punctate ground sculpture only, otherwise unsculptured. Waist segments strongly longitudinally rugose to reticulate-rugose. Ground sculpture on head, mesosoma, and waist segments generally faint. First gastral tergite covered completely with very conspicuous punctate sculpture, appearing matt. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. First gastral tergite without appressed pubescence. Anterior edges of antennal scapes with subdecumbent to erect standing hairs. Body a uniform brown to dark brown colour.

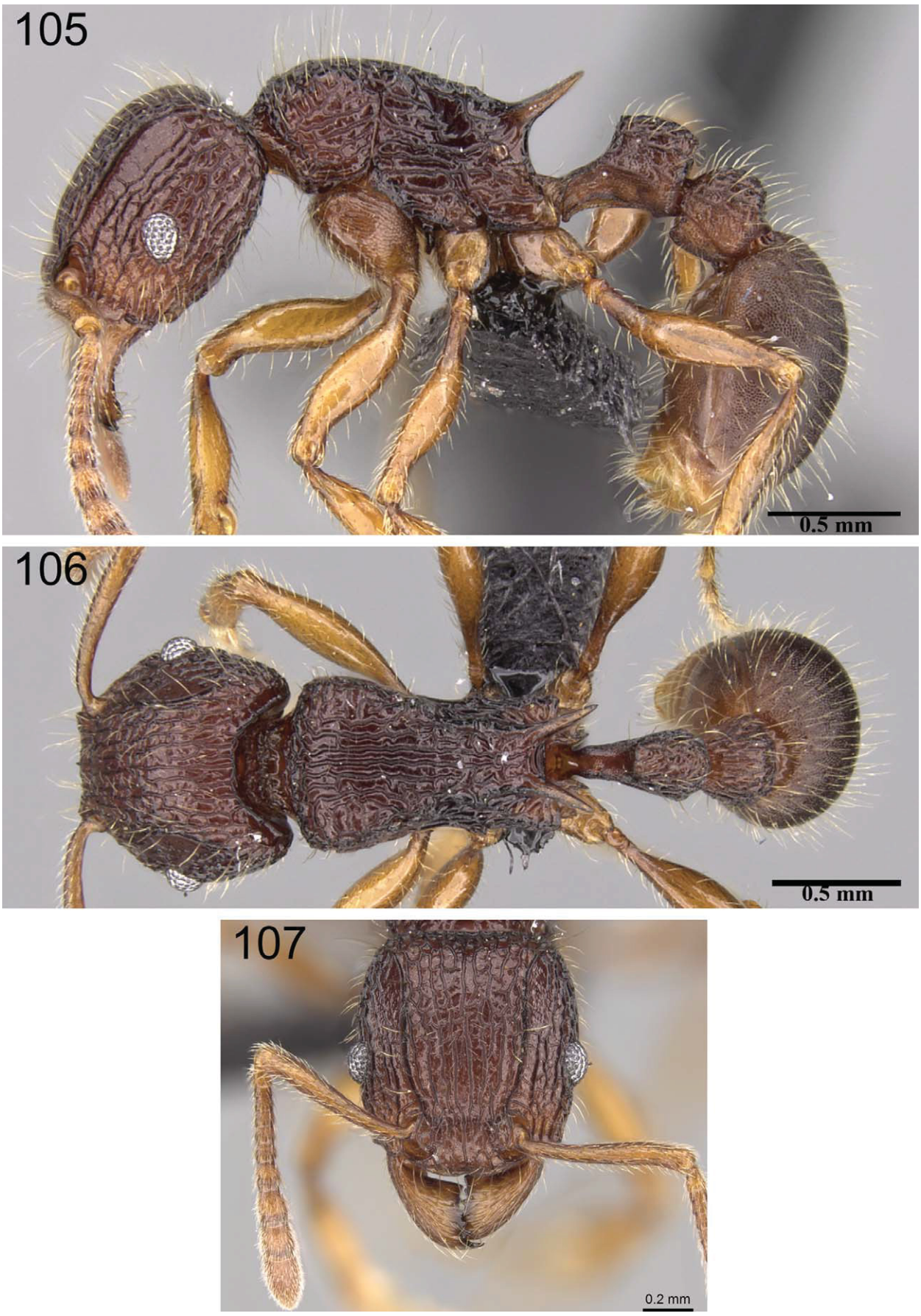
Notes

Tetramorium jedi is mainly distributed in the northeast of the island of Madagascar from Anjanaharibe north to Binara. Surprisingly, the species is also known from Ambalagoavy, which is located much further south. The available material was sampled from lowland rainforests at elevations between 240 to 800 m. The species appears to be ground-active.

As mentioned in the diagnosis above, *T. jedi* is unique in the *T. tortuosum* group because of the pronounced and very distinct sculpture on the first gastral tergite, which covers the whole tergite.

Etymology

This new species is named after the fictional, noble, and wise guardians of peace from the "Star Wars" universe created by George Lucas. The species epithet is an arbitrary combination of letters.



FIGURES 105–107. *T. jedi*, holotype (CASENT0043578). **105.** Body in profile. **106.** Body in dorsal view. **107.** Head in full-face view.

Material examined

MADAGASCAR: Antsiranana, Forêt Ambanitaza, 26.1 km 347° Antalaha, 14.67933 S, 50.18367 E, 240 m, rainforest, 26.XI.2004 (*B.L. Fisher*); Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, 13.26333 S, 49.60333 E, 725-800 m, rainforest, 3.–4.XII.2003 (*B.L. Fisher*); Antsiranana, Makirovana forest, 14.17066 S, 49.95409 E, 415 m, rainforest, 29.IV.2011 (*B.L. Fisher et al.*); Antsiranana, Makirovana forest, 14.16666 S, 49.95 E, 715 m, rainforest, 2.V.2011 (*B.L. Fisher et al.*); Antsiranana, Makirovana forest, 14.17066 S, 49.95409 E, 225 m, rainforest, 4.V.2011 (*B.L. Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, 15.–18.XI.2003 (*B.L. Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14.4367 S, 49.775 E, 450 m, rainforest, 12.–25.XI.2003 (*B.L. Fisher et al.*); Fianarantsoa, Foret d'Ambalagoavy Nord, Ikongo, Ambatombe, 21.8275 S, 47.33889 E, 625 m, 1.XII.2000 (*R. Harin'Hala & M.E. Irwin*); Toamasina, Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 15.18833 S, 49.615 E, 470 m, rainforest, 8.–12.III.2003 (*B.L. Fisher & C. Griswold*).

Tetramorium pleganon Bolton, 1979

(Figs. 48, 108, 109, 110, 142)

Tetramorium pleganon Bolton, 1979:146. Holotype worker, MADAGASCAR, Antsiranana, 84 km SW Sambava on road to Andapa, 70–160 m, degraded forest, strays on path, AB 43, 17.II.1977 (*W.L. & D.E. Brown*) (MCZ: CASENT0280587) [examined]. Paratypes, three workers with same data as holotype (BMNH: CASENT0102399; MCZ: CASENT0280588) [examined].

Diagnosis

Tetramorium pleganon is easily recognisable within the *T. tortuosum* group in the Malagasy region due to the character combination of: propodeal spines long to very long (PSLI 37–44); petiolar node wider than long (DPeI 111–118); dorsum of petiolar node strongly rugose; first gastral tergite with superficial, fine, reticulate-punctate sculpture, ranging from basal third to more than half of tergite.

Description

HL 0.87–1.05 (0.93); HW 0.85–1.02 (0.91); SL 0.61–0.73 (0.66); EL 0.18–0.23 (0.19); PH 0.43–0.56 (0.48); PW 0.59–0.79 (0.69); WL 1.07–1.31 (1.17); PSL 0.32–0.43 (0.37); PTL 0.22–0.31 (0.25); PTH 0.34–0.44 (0.37); PTW 0.26–0.34 (0.29); PPL 0.27–0.34 (0.29); PPH 0.31–0.43 (0.35); PPW 0.34–0.43 (0.38); CI 96–99 (97); SI 71–74 (73); OI 20–23 (21); DMI 52–61 (59); LMI 38–43 (41); PSLI 37–44 (39); PeNI 40–44 (42); LPeI 63–73 (67); DPeI 111–118 (115); PpNI 52–61 (55); LPpI 80–89 (83); DPpI 122–137 (129); PPI 126–138 (130) (14 measured).

Head longer than wide (CI 96–99); posterior head margin moderately concave. Anterior clypeal margin medially impressed, often weakly so. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, shallow to moderately deep, and broad, without defined posterior and ventral margins. Antennal scapes short, not reaching posterior head margin (SI 71–74). Eyes small to moderate in size (OI 20–23). Mesosomal outline in profile weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–43). Propodeal spines very long, spinose and acute (PSLI 37–44); propodeal lobes short, triangular, and acute. Petiolar node in profile rectangular nodiform, approximately 1.1 to 1.2 times higher than long (LPeI 63–73), anterior and posterior faces approximately parallel, anterodorsal margin situated higher than posterodorsal, dorsum weakly tapering backwards posteriorly; node in dorsal view approximately 1.1 to 1.2 times wider than long (DPeI 111–118). Postpetiole in profile rounded, approximately 1.1 to 1.3 times higher than long (LPpI 80–89); in dorsal view around 1.2 to 1.4 times wider than long (DPpI 122–137). Postpetiole in profile approximately as voluminous as petiolar node, in dorsal view 1.2 to 1.4 times wider than petiolar node (PPI 126–138). Mandibles generally finely to strongly striate; clypeus longitudinally

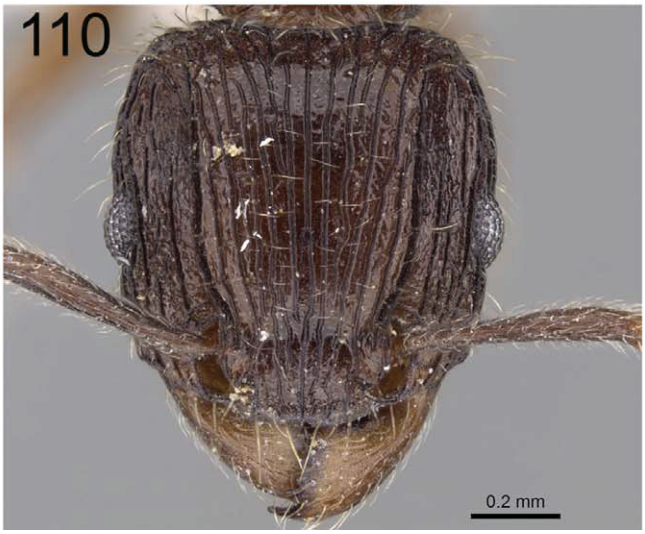
rugose, with four to nine rugae, median ruga always present and distinct, remaining rugae variably developed, usually weaker; cephalic dorsum between frontal carinae with 11 to 14 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted and none with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose, very rarely with cross-meshes. Ground sculpture on head generally feeble. Mesosoma laterally and dorsally distinctly longitudinally rugose, lateral mesosoma sometimes weaker sculptured than dorsum. Forecoxae generally unsculptured, smooth, and shining, sometimes with superficial sculpture. Ground sculpture on mesosoma generally faint to absent. Waist segments strongly rugose dorsally, laterally rugose sculpture much weaker; both waist segments with very conspicuous reticulate-punctate ground sculpture. First gastral tergite with fine, dense, reticulate-punctate ground sculpture, ranging from basal third to more than half of tergite. All dorsal surfaces of body with abundant, long, and fine standing hairs; first gastral tergite with mix of moderately long appressed to decumbent hairs and more abundant and longer suberect to erect hairs. Anterior edges of antennal scapes with decumbent to suberect hairs. Body a uniform very dark brown to black colour, appendages often lighter in colour.

Notes

Tetramorium pleganon possesses a comparatively wide distribution in Madagascar since it is found in many localities from Zombitse and Kalambatrita in the south up to Ambato and Antsahabe in the north. It appears to be comparatively flexible in its habitat preferences. Most of the localities where it was encountered consisted of rainforest, montane rainforest, or tropical dry forest, but the number of specimens collected in these habitats was comparatively low. In contrast, the largest number of examined specimens were sampled in Uapaca woodland, savannah grassland, and degraded forests, indicating that *T. pleganon* might be more successful in disturbed and open habitats than in dense forests.

In Bolton's (1979) revision *T. pleganon* was easily diagnosable and recognisable from all other Malagasy *Tetramorium* due to its 11-segmented antennae and the sculptured first gastral tergite. However, our ongoing revision has revealed several species with 11-segmented antennae and sculpture on the first gastral tergite, indicating this character combination is more common than previously thought, and is certainly not unique to *T. pleganon*. Nevertheless, within the *T. tortuosum* group there are different types of sculpture observable on the first gastral tergite, and the reticulate-punctate ground sculpture seen in *T. pleganon* places it well within the *T. jedi* complex. Within this complex, *T. pleganon* is unlikely to be misidentified with *T. jedi* since the latter species has a completely sculptured tergite with very strongly developed and conspicuous reticulate-punctate sculpture. In *T. pleganon* the sculpture is well-developed, too, but much more superficial, and does not cover the whole tergite. In addition, the petiolar node of *T. pleganon* is distinctly wider than long (DPeI 111–188), which contrasts with the clearly longer than wide node of *T. jedi* (DPeI 79–85). *Tetramorium avaratra*, the third species of the complex, is morphologically much closer to *T. pleganon*, but differs in propodeal spine length, petiolar node shape, and general development of sculpture on waist segments and gaster. *Tetramorium avaratra* has generally much shorter propodeal spines (PSLI 27–34 without the Nosy Be specimens, PSLI 27–37 with the Nosy Be material) than *T. pleganon* (PSLI 37–44). Also, the petiolar node is higher and wider in *T. avaratra* (LPeI 54–66; DPeI 126–137) than in *T. pleganon* (LPeI 63–73; DPeI 111–118), and the latter species has much better developed sculpture on the waist segments and the first gastral tergite. As noted in the description of *T. avaratra*, both species overlap in their distribution, and are found living in sympatry in Ankarana. However, both species display their species-characteristics in this locality, and can be well separated from each other by the diagnostics provided above.

Despite this wide distribution range and relative flexibility in habitat preference, *T. pleganon* is morphologically very stable throughout its range with very little variation in morphometry, shape, or colour. The morphological similarities with *T. dysalum*, as well as the potentially erroneous placement of *T. avaratra* and *T. pleganon* within the *T. tortuosum* species group, are discussed in detail in the description of *T. avaratra*.



FIGURES 108–110. *T. pleganon*, holotype (CASENT0280587). **108.** Body in profile. **109.** Body in dorsal view. **110.** Head in full-face view.

Material examined

MADAGASCAR: Antananarivo, Réserve Spéciale d'Ambohitantely, Forêt d Ambohitantely, 20.9 km 72° NE d Ankazobe, 18.22528 S, 47.28683 E, 1410 m, montane rainforest, 17.–22.IV.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Forêt Ambato, 26.6 km 33° Ambanja, 13.4645 S, 48.55167 E, 150 m, rainforest, 8.–10.XII.2004 (*B.L. Fisher*); Antsiranana, Ampasindava, Forêt d'Ambilanivy, 3.9 km 181° S Ambaliha, 13.79861 S, 48.16167 E, 600 m, rainforest, 4.–9.III.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Andapa, 14° 40' S, 49° 39' E, 500 m, degraded forest, 26.I.1991 (*G.D. Alpert*); Antsiranana, 84 km SW Sambava on road to Andapa, 70–160 m, degraded forest, 17.II.1977 (*W.L. & D.E. Brown*); Antsiranana, Res. Ankarana, 12° 54' S, 49° 6' E, 100 m, tropical dry forest, 22.VIII.1992 (*G.D. Alpert*); Antsiranana, Forêt d' Antsahabe, 11.4 km 275° W Daraina, 13.21167 S, 49.55667 E, 550 m, tropical dry forest, 12.XII.2003 (*B.L. Fisher*); Antsiranana, R.S. Manongarivo, 10.8 km 229° SW Antanambao, 13.96167 S, 48.43333 E, 400 m, rainforest, 8.XI.1998 (*B.L. Fisher*); Antsiranana, R.S. Manongarivo, 12.8 km 228° SW Antanambao, 13.97667 S, 48.42333 E, 780 m, rainforest, 11.–17.X.1998 (*B.L. Fisher*); Antsiranana, Makirovana forest, 14.17066 S, 49.95409 E, 415 m, rainforest, 28.–29.IV.2011 (*B.L. Fisher et al.*); Fianarantsoa, Antapia II Non Protected Area, 26.47 km SW Ambositra, 20.71889 S, 47.0867 E, 1494 m, Uapaca woodland, 4.–6.II.2010 (*A. Ravelomanana*); Fianarantsoa, Antohatsahomby I Non Protected Area, 22.77 km NW Ambatofinandrahana, 20.55056 S, 46.58562 E, 1550 m, Uapaca woodland, 15.–17.III.2010 (*A. Ravelomanana*); Fianarantsoa, Mampiarika III Non Protected Area, 28.93 km SW Ambositra, 20.73583 S, 47.08399 E, 1487 m, Uapaca woodland, 1.–2.II.2010 (*A. Ravelomanana*); Fianarantsoa, Soanierenana I Non Protected Area, 25.33 km SW Ambositra, 20.72139 S, 47.10994 E, 1723 m, savannah grassland, 6.–8.II.2010 (*A. Ravelomanana*); Mahajanga, Parc National d'Ankarafantsika, Forêt de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, 16.22806 S, 47.14361 E, 135 m, tropical dry forest, 2.–8.IV.2001 (*B.L. Fisher, C. Griswold et al.*); Mahajanga, Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, 16.26722 S, 47.04861 E, 210 m, tropical dry forest, 9.–14.IV.2001 (*B.L. Fisher, C. Griswold et al.*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.84773 S, 48.29568 E, 1000 m, montane rainforest, 5.–8.III.2007 (*B.L. Fisher et al.*); Toamasina, Manakambahiny, near Vavatenina Forest, 17.46667 S, 49.35 E, 9.II.1995 (*A. Pauly*); Toamasina, Morarano-Chrome, 17.75 S, 47.98333 E, forest, 1.I.1992 (*A. Pauly*); Toamasina, S.F. Tampolo, 10 km NNE Fenoarivo Atn., 17.2825 S, 49.43 E, 10 m, littoral rainforest, 10.IV.1997 (*B.L. Fisher*); Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18.26667 S, 45.40667 E, 1050 m, montane rainforest, 13.–17.I.2003 (*B.L. Fisher et al.*); Toliara, Réserve Spéciale Kalambatritra, 23.4185 S, 46.4583 E, 1365 m, grassland, 8.II.2009 (*B.L. Fisher et al.*).

Tetramorium noeli species complex

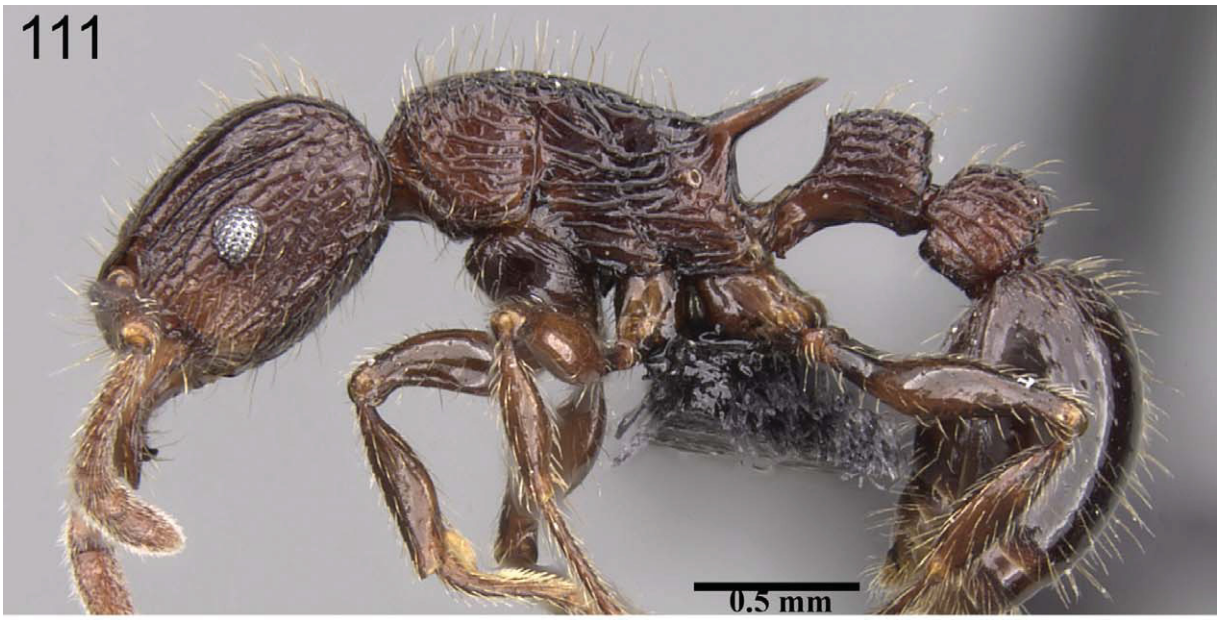
This species complex contains the species *T. ambanizana*, *T. aherni*, *T. singletonae*, and *T. noeli*. The characters that define the complex are the lack of sculpture on the forecoxae and the presence of basigastral costulae on the first gastral tergite.

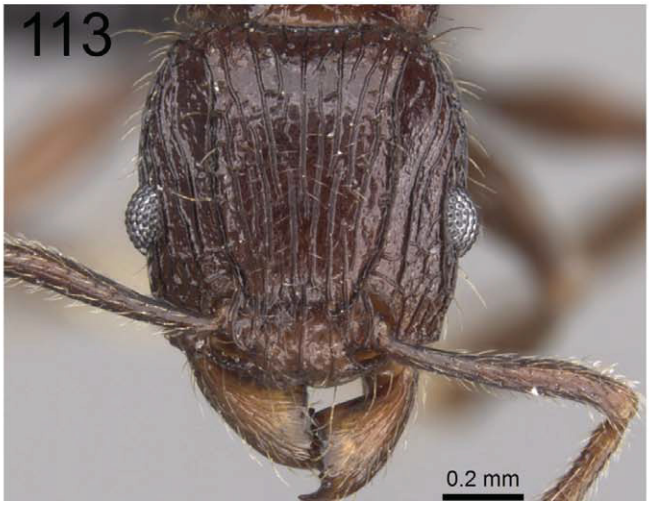
The four species of this complex appear to be morphologically close to each other, and it is likely that they represent a natural group with shared common ancestry.

Tetramorium aherni Hita Garcia & Fisher sp. n.

(Figs. 34, 36, 37, 111, 112, 113, 142)

Holotype worker, MADAGASCAR, Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, sifted litter (leaf mold, rotten wood), collection code BLF08872, 15.–18.XI.2003 (*B.L. Fisher et al.*) (CASC: CASENT0045755). Paratypes, 15 workers with same data as holotype (BMNH: CASENT0045607; CASC: CASENT0045595; CASENT0045603; CASENT0045675; CASENT0045679; CASENT0045687; CASENT0045696; CASENT0045750; CASENT0045766; CASENT0045771; CASENT0045774; CASENT0045779; MCZ: CASENT0045599; MHNG: CASENT0045761; NHMB: CASENT0045746).





FIGURES 111–113. *T. aherni*, holotype (CASENT0045755). **111.** Body in profile. **112.** Body in dorsal view. **113.** Head in full-face view.

Diagnosis

Tetramorium aherni is easily distinguishable within the species group due to the following character combination: eyes moderate to large (OI 22- 24); propodeal spines very long (PSLI 41–45); petiolar node with anterodorsal and posterodorsal margins at about the same height, dorsum flat to weakly convex.

Description

HL 0.91–0.98 (0.93); HW 0.82–0.89 (0.84); SL 0.67–0.74 (0.71); EL 0.19–0.21 (0.20); PH 0.44–0.52 (0.46); PW 0.62–0.69 (0.64); WL 1.11–1.21 (1.15); PSL 0.37–0.42 (0.40); PTL 0.30–0.35 (0.32); PTH 0.34–0.38 (0.36); PTW 0.27–0.31 (0.28); PPL 0.31–0.34 (0.32); PPH 0.37–0.40 (0.38); PPW 0.34–0.39 (0.36); CI 90–92 (90); SI 81–86 (84); OI 22–24 (23); DMI 54–57 (56); LMI 39–43 (40); PSLI 41–45 (43); PeNI 42–46 (44); LPeI 84–93 (89); DPeI 86–94 (89); PpNI 53–60 (56); LPpI 82–87 (84); DPpI 106–117 (113); PPI 121–133 (128) (twelve measured).

Head distinctly longer than wide (CI 90–92); posterior head margin concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, moderately deep and broad but without defined ventral margins. Antennal scapes of moderate length, not reaching posterior head margin (SI 81–86). Eyes small to moderate (OI 22–24). Mesosomal outline in profile weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 39–43). Propodeal spines very long, spinose, and acute (PSLI 41–45); propodeal lobes well-developed, triangular to elongate-triangular, and acute. Petiolar node in profile rectangular nodiform, approximately 1.1 to 1.2 times higher than long (LPeI 84–93), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height, dorsum flat to weakly convex; node in dorsal view approximately 1.1 times longer than wide (DPeI 86–94). Postpetiole in profile subglobular, approximately 1.1 to 1.2 times higher than long (LPpI 82–87); in dorsal view around 1.1 to 1.2 times wider than long (DPpI 106–117). Postpetiole in profile higher than petiolar node and generally appearing slightly more voluminous, in dorsal view approximately 1.2 to 1.3 times wider than petiolar node (PPI 121–133). Mandibles longitudinally rugose/rugulose, sometimes weakly so, sometimes partly sculptured and partly unsculptured; clypeus longitudinally rugose, with three to eight rugae, median ruga always present, remaining rugae variably developed; cephalic dorsum between frontal carinae with 8 to 11 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted and none with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose with very few cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae unsculptured, smooth, and shining with very weak, superficial ground sculpture (punctate or rugulose). Waist segments strongly longitudinally rugose, more irregular dorsally than laterally. Base of first gastral tergite distinctly costulate, remainder of gaster unsculptured, smooth and shining. Ground sculpture generally faint to absent everywhere on body. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with suberect to erect hairs. Body of uniform dark brown to black colour.

Notes

Tetramorium aherni is known from Befingotra, Marojejy, and Makirovana in the north-eastern part of Madagascar, but also from Ambalagoavy, which is situated much further south in eastern Madagascar. The species is only found in lowland or montane rainforests ranging from 450 to 900 m elevation, and seems to prefer the leaf litter stratum.

Inside the *T. noeli* complex, *T. aherni* can be easily distinguished from *T. ambanizana*, *T. noeli*, and *T. singletonae*. The latter species has much smaller eyes (OI 16–17) and shorter propodeal spines (PSLI 27- 29) than *T. aherni* (OI 22–24; PSLI 41–45). In addition, *T. ambanizana* and *T. noeli* have a differently shaped petiolar node with the posterodorsal margin situated much higher than the anterodorsal margin, whereas *T. aherni* has the anterodorsal and posterodorsal margins at about the same height.

Etymology

The new species is dedicated to Dan Ahern for his contribution to the Madagascar Project.

Material examined

MADAGASCAR: Antsiranana, 6.5 km SSW Befingotra, Rés. Anjanaharibe-Sud, 14.75 S, 49.5 E, 875 m, rainforest, 19.–20.X.1994 (*B.L. Fisher*); Antsiranana, Makirovana Forest, 14.1651 S, 49.9477 E, montane rainforest, 30.IV.–1.V.2011 (*B.L. Fisher et al.*); Antsiranana, Makirovana Forest, 14.16044 S, 49.95216 E, 550 m, rainforest,

1.–2.V.2011 (*B.L. Fisher et al.*); Antsiranana, Makirovana Forest, 14.16666 S, 49.95 E, 715 m, rainforest, 1.–2.V.2011 (*B.L. Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 14.43667 S, 49.775 E, 450 m, rainforest, 12.–15.XI.2003 (*B.L. Fisher et al.*); Antsiranana, Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 14.435 S, 49.76 E, 775 m, rainforest, 15.–18.XI.2003 (*B.L. Fisher et al.*); Fianarantsoa, Foret d'Ambalagoavy Nord, Ikongo, Ambatombe, 21.8275 S, 47.33889 E, 625 m, 1.XII.2000 (*R. Harin'Hala & M.E. Irwin*).

Tetramorium ambanizana Hita Garcia & Fisher sp. n.

(Figs. 42, 43, 114, 115, 116, 142)

Holotype worker, MADAGASCAR, Toamasina, 5.3 km SSE Ambanizana, Andranobe, 15.66667 S, 49.96667 E, 425 m, rainforest, leaf litter (sifted mold, rotten wood), collection code BLF00926, 21.XI.2003 (*B.L. Fisher*) (CASC: CASENT0189238). Paratypes, four workers with same data as holotype (CASC: CASENT0189214, CASENT0218048, CASENT0218050, CASENT0270779).

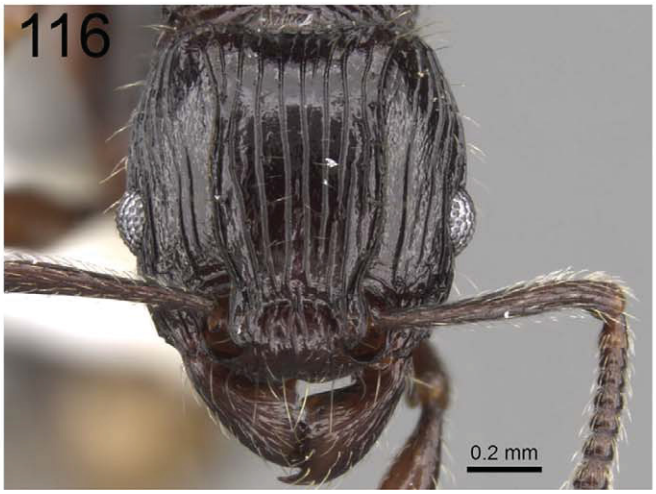
Diagnosis

Within the *T. noeli* species complex *T. ambanizana* can be recognised by the following character combination: head weakly longer than wide (CI 97–98); propodeal spines extremely long (PSLI 60–65); petiolar node rectangular nodiform with the posterodorsal margin situated much higher than the anterodorsal margin, and the dorsum convex; postpetiole in profile around 1.2 to 1.3 times higher than long (LPpI 77–81), and in dorsal view approximately 1.1 times wider than long (DPpI 104–112).

Description

HL 0.85–0.95 (0.92); HW 0.82–0.93 (0.90); SL 0.68–0.76 (0.73); EL 0.20–0.21 (0.20); PH 0.43–0.48 (0.46); PW 0.61–0.69 (0.66); WL 1.08–1.23 (1.17); PSL 0.55–0.58 (0.57); PTL 0.31–0.35 (0.33); PTH 0.38–0.43 (0.40); PTW 0.26–0.30 (0.28); PPL 0.33–0.35 (0.34); PPH 0.41–0.46 (0.43); PPW 0.36–0.38 (0.37); CI 97–98 (98); SI 78–83 (81); OI 21–24 (22); DMI 56–58 (57); LMI 38–41 (39); PSLI 60–65 (62); PeNI 40–43 (42); LPeI 79–83 (81); DPeI 82–86 (84); PpNI 54–58 (56); LPpI 77–81 (79); DPpI 104–112 (108); PPI 127–138 (134) (five measured).

Head weakly longer than wide (CI 97–98); posterior head margin moderately concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, moderately deep, but narrow and without defined posterior and ventral margins. Antennal scapes short to moderate, not reaching posterior head margin (SI 78–83). Eyes small to moderate (OI 21–24). Mesosomal outline in profile weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–41). Propodeal spines extremely long, spinose, and acute (PSLI 60–65); propodeal lobes well-developed, triangular to elongate-triangular, and acute. Petiolar node in profile rectangular nodiform but comparatively high, approximately 1.2 to 1.3 times higher than long (LPeI 79–83), anterior and posterior faces approximately parallel, posterodorsal margin situated higher than anterodorsal, dorsum convex; node in dorsal view approximately 1.2 times longer than wide (DPeI 82–86). Postpetiole in profile subglobular and anteroposteriorly compressed, approximately 1.2 to 1.3 times higher than long (LPpI 77–81); in dorsal view around 1.1 times wider than long (DPpI 104–112). Postpetiole in profile higher and less voluminous than petiolar node, in dorsal view approximately 1.3 to 1.4 times wider than petiolar node (PPI 127–138). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugulose, with one to six rugulae, median rugula always present, remaining rugulae variably developed; cephalic dorsum between frontal carinae with six to nine longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted and none with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose, very rarely with cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae unsculptured, smooth, and shining, with weak, superficial ground sculpture. Waist segments strongly and very regularly longitudinally rugose, rugae absent from anterior face, but running unbroken from one side to other through posterior face. Base of first gastral tergite distinctly costulate, remainder of gaster unsculptured, smooth and shining. Ground sculpture generally faint to absent everywhere on body. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs; first gastral tergite without appressed pubescence. Anterior edges of antennal scapes suberect to erect hairs. Body uniform dark brown to black in colour.



FIGURES 114–116. *T. ambanizana*, holotype (CASENT0189238). **114.** Body in profile. **115.** Body in dorsal view. **116.** Head in full-face view.

Notes

At present, *T. ambanizana* is only known from the type series from Ambanizana where it was collected from rainforest at an elevation of 425 m. The new species appears to inhabit leaf litter.

Within the species complex its petiolar node shape distinguishes it from *T. aherni* and *T. singletonae* since the latter two have a node with the anterodorsal and posterodorsal margins at about the same height. The node of *T. ambanizana* has a posterodorsal margin situated much higher than the anterodorsal margin. This node development is shared with the remaining species, *T. noeli*, which is generally fairly similar to *T. ambanizana*. Both are described as new and distinct species here, but it is possible that they are conspecific. Their general appearance is very much alike, and differentiating between the two requires measuring a few key characters. *Tetramorium ambanizana* is only known from the type locality, whereas *T. noeli* is found in several localities further north. This could mean that the first might be a geographic variation of the latter. However, we consider the following morphometric differences sufficient to consider them different species until more material, especially from *T. ambanizana*, becomes available. The head of *T. noeli* is always distinctly longer than wide (CI 92–95) while it is only weakly longer than wide in *T. ambanizana* (CI 97–98). In addition, both species have extremely long propodeal spines, but the spines of *T. ambanizana* are still much longer (PSLI 60–65) than the spines of *T. noeli* (PSLI 38–48). The third separating character is the shape of the postpetiole, which is relatively higher and broader in *T. noeli* (LPpI 68–72; DPpI 119–129) than in *T. ambanizana* (LPpI 77–81; DPpI 104–112).

Etymology

The new species is named after the type locality. The species epithet is a noun in apposition, and thus invariant.

Material examined

MADAGASCAR: Toamasina, 5.3 km SSE Ambanizana, Andranobe, 15.66667 S, 49.96667 E, 425 m, rainforest, 21.XI.2003 (*B.L. Fisher*).

Tetramorium noeli Hita Garcia & Fisher sp. n.

(Figs. 35, 40, 41, 117, 118, 119, 142)

Holotype worker, MADAGASCAR, Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, 13.26333 S, 49.60333 E, 800 m, rainforest, sifted litter, (leaf mold, rotten wood), collection code BLF09656, 3.XII.2003 (*B.L. Fisher*) (CASC: CASENT0043554). Paratypes, nine workers with same data as holotype (BMNH: CASENT0043563; CASC: CASENT0043546; CASENT0043547; CASENT0043549; CASENT0043550; CASENT0043559; CASENT0043571; CASENT0043577; CASENT0043688); and one worker with same data as holotype but collected ex rotten log the 20.XI.2004 and collection code BLF10901 (MCZ: CASENT0053894).

Diagnosis

The following character set distinguishes *T. noeli* from the remainder of the species group: head distinctly longer than wide (CI 92–95); propodeal spines very long to extremely long (PSLI 38–48); petiolar node rectangular nodiform with the posterodorsal margin situated higher than the anterodorsal margin, and the dorsum convex; postpetiole in lateral view approximately 1.4 to 1.5 times higher than long (LPpI 68–72), and in dorsal view around 1.2 to 1.3 times wider than long (DPpI 119–129).

Description

HL 0.85–1.00 (0.95); HW 0.79–0.94 (0.89); SL 0.64–0.77 (0.72); EL 0.18–0.22 (0.21); PH 0.45–0.55 (0.50); PW 0.65–0.79 (0.71); WL 1.11–1.44 (1.24); PSL 0.33–0.46 (0.41); PTL 0.32–0.39 (0.36); PTH 0.38–0.47 (0.43); PTW 0.26–0.32 (0.30); PPL 0.31–0.35 (0.33); PPH 0.43–0.50 (0.46); PPW 0.37–0.44 (0.41); CI 92–95 (94); SI 79–85 (81); OI 22–24 (23); DMI 55–59 (57); LMI 37–43 (57); PSLI 38–48 (43); PeNI 39–46 (42); LPeI 80–88 (84); DPeI 78–86 (82); PpNI 53–62 (57); LPpI 68–72 (71); DPpI 119–129 (124); PPI 132–145 (137) (15 measured).

Head distinctly longer than wide (CI 92–95); posterior head margin moderately concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, moderately deep, but narrow and without defined posterior and ventral margins. Antennal scapes short to moderate, not reaching posterior head margin (SI 79–85). Eyes of

moderate size (OI 22–24). Mesosomal outline in profile weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–43). Propodeal spines very long, spinose and acute (PSLI 38–48); propodeal lobes well-developed, triangular to elongate-triangular, and acute. Petiolar node in profile rectangular nodiform but comparatively high, approximately 1.1 to 1.3 times higher than long (LPeI 80–88), anterior and posterior faces approximately parallel, posterodorsal margin situated higher than anterodorsal, dorsum convex; node in dorsal view approximately 1.2 to 1.3 times longer than wide (DPeI 78–86). Postpetiole in profile comparatively high and anteroposteriorly compressed, approximately 1.4 to 1.5 times higher than long (LPpI 68–72); in dorsal view around 1.2 to 1.3 times wider than long (DPpI 119–129). Postpetiole in profile noticeably higher and less voluminous than petiolar node, in dorsal view approximately 1.3 to 1.5 times wider than petiolar node (PPI 132–145). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose, with three to eight rugae, median ruga always present and distinct, remaining rugae variably developed; cephalic dorsum between frontal carinae with 6 to 12 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted and none with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose to reticulate-rugose. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae unsculptured, smooth, and shining, with weak, superficial ground sculpture. Waist segments strongly and very regularly longitudinally rugose, rugae absent from anterior face, but running unbroken from one side to the other through posterior face. Base of first gastral tergite distinctly costulate, remainder of gaster unsculptured, smooth and shining. Ground sculpture generally faint to absent everywhere on body. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs; first gastral tergite without appressed pubescence. Anterior edges of antennal scapes suberect to erect hairs. Body a uniform very dark brown to black colour.

Notes

Tetramorium noeli appears to be moderately common in the tropical dry forests and rainforests of the northeastern tip of Madagascar. Currently its distribution extends from Ambanitaza north to Montagne des Français, but it might well occur in other forest localities in northeastern Madagascar not yet explored. The new species appears to be a leaf litter inhabitant on the basis of available collection data.

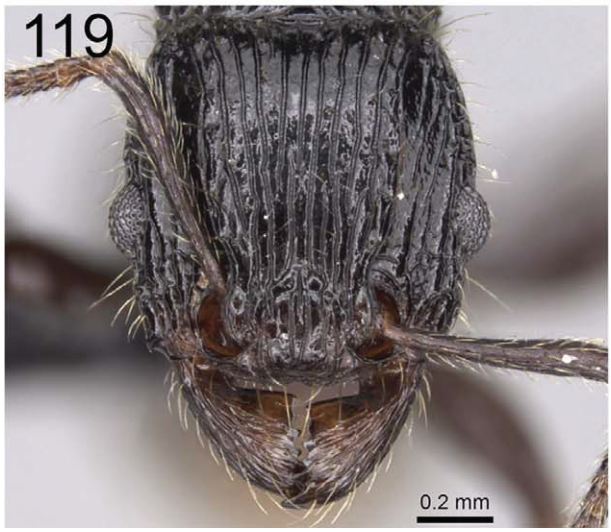
Within the *T. noeli* species complex, *T. noeli* cannot be confused with either *T. aherni* or *T. singletonae* since these have a petiolar node shape with the anterodorsal and posterodorsal margins at about the same height, whereas the node of *T. noeli* has a posterodorsal margin which is situated much higher than the anterodorsal. The fourth species of the complex, *T. ambanizana*, has a node shape similar to *T. noeli*, and both species are morphologically very similar. Indeed, as noted in the description of *T. ambanizana*, it is possible that both are conspecific. However, we treat them as distinct species here, and both differ in the length of the propodeal spines and the shape of the head and postpetiole. In *T. noeli* the head is distinctly longer than wide (CI 92–95), whereas the head of *T. ambanizana* is only weakly longer than wide (CI 97–98). Additionally, despite both species having extremely long propodeal spines, this character is better developed in *T. ambanizana* (PSLI 60–65) than in *T. noeli* (PSLI 38–48). Also, the postpetiole of the latter species is relatively higher (LPpI 68–75) and broader (DPpI 119–129) than in *T. ambanizana* (LPpI 77–81; DPpI 104–112).

Etymology

The new species is dedicated to Noel Hita Garcia from Remscheid, Germany.

Material examined

MADAGASCAR: Antsiranana, Forêt Ambanitaza, 26.1 km 347° Antalaha, 14.67933 S, 50.18367 E, 240 m, rainforest, 26.XI.2004 (*B.L. Fisher*); Antsiranana, Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 12.53444 S, 49.1795 E, 925 m, montane rainforest, 20.–26.I.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Réserve Spéciale de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, 12.86361 S, 49.22583 E, 210 m, tropical dry forest, 16.–21.II.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, 13.26333 S, 49.60333 E, 800 m, rainforest, 3.XII.2003 (*B.L. Fisher*); Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, 13.26333 S, 49.60333 E, 800 m, rainforest, 20.XI.2004 (*B.L. Fisher*); Antsiranana, Montagne des Français, 7.2 km 142° SE Antsiranana, 12.32278 S, 49.33817 E, 180 m, tropical dry forest, 22.–28.II.2001 (*B.L. Fisher, C. Griswold et al.*); Antsiranana, Makirovana forest, 14.1707 S, 49.9541 E, 415 m, rainforest, 28.–29.IV.2011 (*B.L. Fisher et al.*); Antsiranana, Makirovana forest, 14.1651 S, 49.9477 E, 900 m, montane rainforest, 30.IV.–1.V.2011 (*B.L. Fisher et al.*); Antsiranana, Makirovana forest, 14.16044 S, 49.95216 E, 550 m, rainforest, 1.–2.V.2011 (*B.L. Fisher et al.*).



FIGURES 117–119. *T. noeli*, holotype (CASENT0043554). **117.** Body in profile. **118.** Body in dorsal view. **119.** Head in full-face view.

Tetramorium singletonae **Hita Garcia & Fisher sp. n.**
(Figs. 30, 32, 38, 39, 120, 121, 122, 142)

Holotype worker, MADAGASCAR, Toamasina, 5.3 km SSE Ambanizana, Andranobe, 15.66667 S, 49.96667 E, 425 m, rainforest, pitfall trap, collection code BLF00906, 19.XI.1993 (*B.L. Fisher*) (CASC: CASENT0247161). Paratypes, five workers with same data as holotype (CASC: CASENT0188733; CASENT0247159; CASENT0270778).

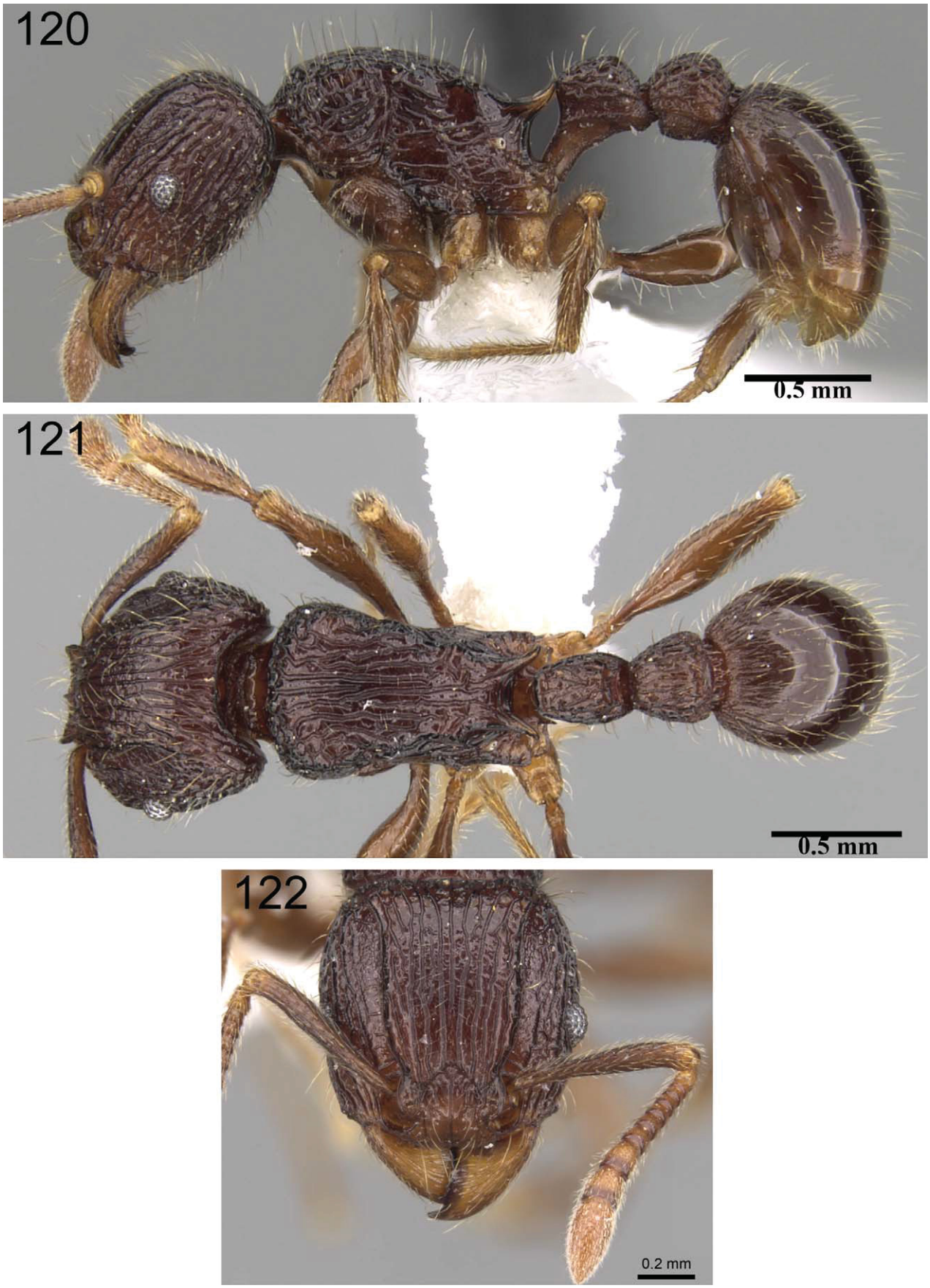
Diagnosis
Tetramorium singletonae is easily recognisable within the *T. noeli* complex by the following combination of characters: eyes very small (OI 16–17); propodeal spines long, but very short for the species group (PSLI 27–29); petiolar node with anterodorsal and posterodorsal margins at about the same height, dorsum flat to weakly convex.

Description
HL 0.90–0.92 (0.91); HW 0.87–0.90 (0.89); SL 0.62–0.66 (0.64); EL 0.14–0.16 (0.15); PH 0.42–0.49 (0.47); PW 0.67–0.69 (0.68); WL 1.10–1.16 (1.13); PSL 0.25–0.27 (0.25); PTL 0.33–0.35 (0.34); PTH 0.33–0.36 (0.33); PTW 0.27–0.29 (0.28); PPL 0.30–0.31 (0.30); PPH 0.34–0.35 (0.34); PPW 0.35–0.37 (0.36); CI 97–98 (98); SI 70–74 (72); OI 16–17 (17); DMI 59–62 (60); LMI 38–44 (41); PSLI 27–29 (28); PeNI 40–42 (41); LPeI 94–106 (101); DPeI 81–85 (83); PpNI 51–54 (53); LPpI 86–91 (89); DPpI 115–122 (118); PPI 126–130 (128) (eight measured).

Head weakly longer than wider (CI 97–98). Anterior clypeal margin with median impression, sometimes weak, but always distinct. Frontal carinae well-developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, but shallow, narrow, and without defined posterior and ventral margins. Antennal scapes comparatively short, not reaching posterior head margin (SI 70–74). Eyes very small (OI 16–17). Mesosomal outline in profile flat, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–44). Propodeal spines with very broad base, up-curved, elongate-triangular, and moderately long (PSLI 27–29); propodeal lobes well-developed, triangular and acute. Petiolar node in profile rectangular nodiform, ranging from weakly longer than high to weakly higher than long (LPeI 94–106), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum flat to weakly convex; node in dorsal view approximately 1.2 times longer than wide (DPeI 81–85). Postpetiole in profile globular, approximately 1.1 times higher than long (LPpI 86–91); in dorsal view around 1.2 times wider than long (DPpI 115–122). Postpetiole in profile appearing approximately as voluminous as petiolar node, in dorsal view approximately 1.2 to 1.3 times wider than petiolar node (PPI 126–130). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose, with three to five rugae; cephalic dorsum between frontal carinae with 8 to 11 longitudinal rugae, most rugae running unbroken from posterior head margin to posterior clypeus, few rugae interrupted or with cross-meshes; lateral and ventral head longitudinally rugose, rarely with cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae unsculptured. Waist segments strongly irregularly longitudinally rugose. Base of first gastral tergite with costulate sculpture, remainder of gaster unsculptured, smooth, and shiny. Ground sculpture generally faint to absent everywhere on body. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. First gastral tergite without distinct, appressed pubescence. Anterior edges of antennal scapes with subdecumbent to erect, standing hairs. Body a uniform brown colour.

Notes
The available material from this new species was sampled from Ambanizana and Amparihibe. Both localities are rainforests located in the northeast of Madagascar at elevations of 425 to approximately 1000 m. *Tetramorium singletonae* appears to live and/or forage on the ground since most specimens were collected from pitfall traps.

Tetramorium singletonae is the species with the shortest antennal scapes (SI 70–74 vs. SI 78–86), smallest eyes (OI 16–17 vs. OI 21–24), and shortest propodeal spines (PSLI 27–29 vs. PSLI 38–65) encountered in the *T. noeli* species complex, and is thus easily recognisable. At first glance *T. singletonae* is also morphologically close to *T. nify* from the *T. andrei* species complex since both have shorter propodeal spines than most other *T. tortuosum* group species and similarly shaped waist segments, but the base of the first gastral tergite is unsculptured in *T. nify*.



FIGURES 120–122. *T. singletonae*, holotype (CASENT0247161). **120.** Body in profile. **121.** Body in dorsal view. **122.** Head in full-face view.

Etymology
The new species is dedicated to Sarah Singleton for her support to promote the discovery and identification of life on earth.

Material examined
MADAGASCAR: Toamasina, 5.3 km SSE Ambanizana, Andranobe, 15.66667 S, 49.96667 E, 425 m, rainforest, 19.XI.1993 (*B.L. Fisher*); Toamasina, Amparihibe, 15° 2' S, 49° 34' E, II.–III.2003 (*K.A. Jackson & D. Carpenter*).

Tetramorium smaug species complex

This complex includes the species *T. adamsi*, *T. latreillei*, *T. marojejy*, *T. nazgul*, *T. sabatra*, and *T. smaug*. They are all characterized by the presence of very strongly developed longitudinal rugae on the forecoxae, and the absence of sculpture on the first gastral tergite (except in some specimens of *T. manongarivo*, which have costulate sculpture on the basal half of the first gastral tergite).

The species within this group can be further divided into those with massive propodeal spines and reduced hairiness (*T. latreillei*, *T. sabatra*, and *T. smaug*), while the remaining three species are much hairier and have less massive propodeal spines (*T. adamsi*, *T. marojejy*, and *T. nazgul*).

Tetramorium adamsi Hita Garcia & Fisher sp. n.
(Figs. 14, 17, 123, 124, 125, 142)

Holotype worker, MADAGASCAR, Antsiranana, R.S. Manongarivo 17.3 km 218° SW Antanambao, 14.02167 S, 48.41833 E, 1580 m, montane rainforest, sifted litter (leaf mold, rotten wood), collection code BLF01970, 27.X.1998 (*B.L. Fisher*) (CASC: CASENT0247345). Paratypes, 21 workers with same data as holotype (BMNH: CASENT0247299; CASC: CASENT0189393; CASENT0218051; CASENT0247290; CASENT0247291; CASENT0247292; CASENT0247293; CASENT0247294; CASENT0247300; CASENT0247304; CASENT0247305; CASENT0247306; CASENT0247307; CASENT0247308; CASENT0247341; CASENT0247342; CASENT0247343; CASENT0247344; MCZ: CASENT0247301; MHNG: CASENT0247297; NHMB: CASENT0247303).

Diagnosis
Tetramorium adamsi can be straightforwardly recognised within the *T. smaug* species complex since it is the only species in which the posterodorsal margin of the petiolar node is situated higher than the anterodorsal margin.

Description
HL 0.94–1.06 (1.01); HW 0.89–1.03 (0.96); SL 0.69–0.82 (0.76); EL 0.17–0.21 (0.19); PH 0.43–0.55 (0.50); PW 0.63–0.78 (0.72); WL 1.13–1.45 (1.30); PSL 0.34–0.51 (0.44); PTL 0.31–0.39 (0.36); PTH 0.34–0.42 (0.38); PTW 0.25–0.31 (0.28); PPL 0.29–0.32 (0.31); PPH 0.34–0.42 (0.38); PPW 0.34–0.39 (0.36); CI 93–97 (95); SI 73–84 (79); OI 18–22 (20); DMI 51–59 (56); LMI 34–40 (38); PSLI 36–50 (43); PeNI 36–41 (39); LPeI 88–97 (93); DPeI 76–84 (79); PpNI 47–54 (50); LPpI 75–86 (81); DPpI 113–126 (117); PPI 116–138 (127) (18 measured).

Head longer than wide (CI 93–97); posterior head margin concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes weakly developed, shallow, and narrow, without defined posterior and ventral margins. Antennal scapes short to moderate in length, not reaching posterior head margin (SI 73–84). Eyes short to moderately sized (OI 18–22). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 34–40). Propodeal spines very long to extremely long, spinose and acute (PSLI 36–50); propodeal lobes well-developed, triangular to elongate-triangular, and usually acute. Petiolar node in profile rectangular nodiform, approximately 1.0 to 1.1 times higher than long (LPeI 81–88), anterior

and posterior faces approximately parallel, posterodorsal margin situated higher than anterodorsal margin, dorsum convex; node in dorsal view approximately 1.2 to 1.3 times longer than wide (DPeI 76–84). Postpetiole in profile subglobular, approximately 1.2 to 1.3 times higher than long (LPpI 75–86); in dorsal view around 1.1 to 1.3 times wider than long (DPpI 113–126). Postpetiole in profile generally appearing less voluminous than petiolar node, in dorsal view between 1.1 to 1.4 times wider than petiolar node (PPI 116–138). Mandibles striate; clypeus longitudinally rugose/rugulose, with four to eight rugae/rugulae, median ruga usually present and distinct, but rarely more conspicuous than other rugae/rugulae; cephalic dorsum between frontal carinae with eight to 13 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted and with cross-meshes; lateral and ventral head mostly reticulate-rugose. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae with well-developed and conspicuous longitudinal rugae. Waist segments strongly rugose. Gaster mostly unsculptured, smooth, and shining, several specimens from higher elevations with distinct costulae on the basal half of first gastral tergite. Ground sculpture generally faint to absent everywhere on body, better developed at higher elevations, but still weak. All dorsal surfaces with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with suberect to erect hairs. Body generally uniformly dark brown to black in colour, sometimes appendages of slightly lighter colour.

Notes

The new species is currently only known from Manongarivo and Bemanevika, where it was collected from montane forest leaf litter at elevations from 1175 to 1860 m. Almost all of the material was sampled in Manongarivo while just one specimen from Bemanevika was available.

Tetramorium adamsi shows a remarkable variation in Manongarivo. The examined material was collected from three sub-localities located at different altitudes separated by few kilometres from each other. The lowest was situated at 1175 m, the middle at 1580, and the highest at 1860 m. The specimens from 1175 m had longer antennal scapes (SI 81–84), longer propodeal spines (PSLI 47–50), and a narrower postpetiole in relation to the petiolar node (PPI 116–125) than specimens from the higher elevations (SI 73–78; PSLI 36–41; PPI 129–138). These differences were fairly constant between the series, and we have considered separating the material into two species. However, the only arguments for separation are morphometric divergences, and apart from this there is a great amount of morphological similarity. For these reasons, we have decided against a split. In addition, we found that on half of the workers from the highest elevation at 1860 m, the basal half of the first gastral tergite is distinctly costulate while it is unsculptured and smooth in the remaining specimens. Sculpture on the first gastral tergite is generally of high diagnostic importance in the *T. tortuosum* group, and could have been a reason to split the *T. adamsi* material. Nevertheless, no other character could separate the sculptured specimens from those collected at the two higher sub-localities. This has convinced us to keep all the material as one variable, but well-defined species.

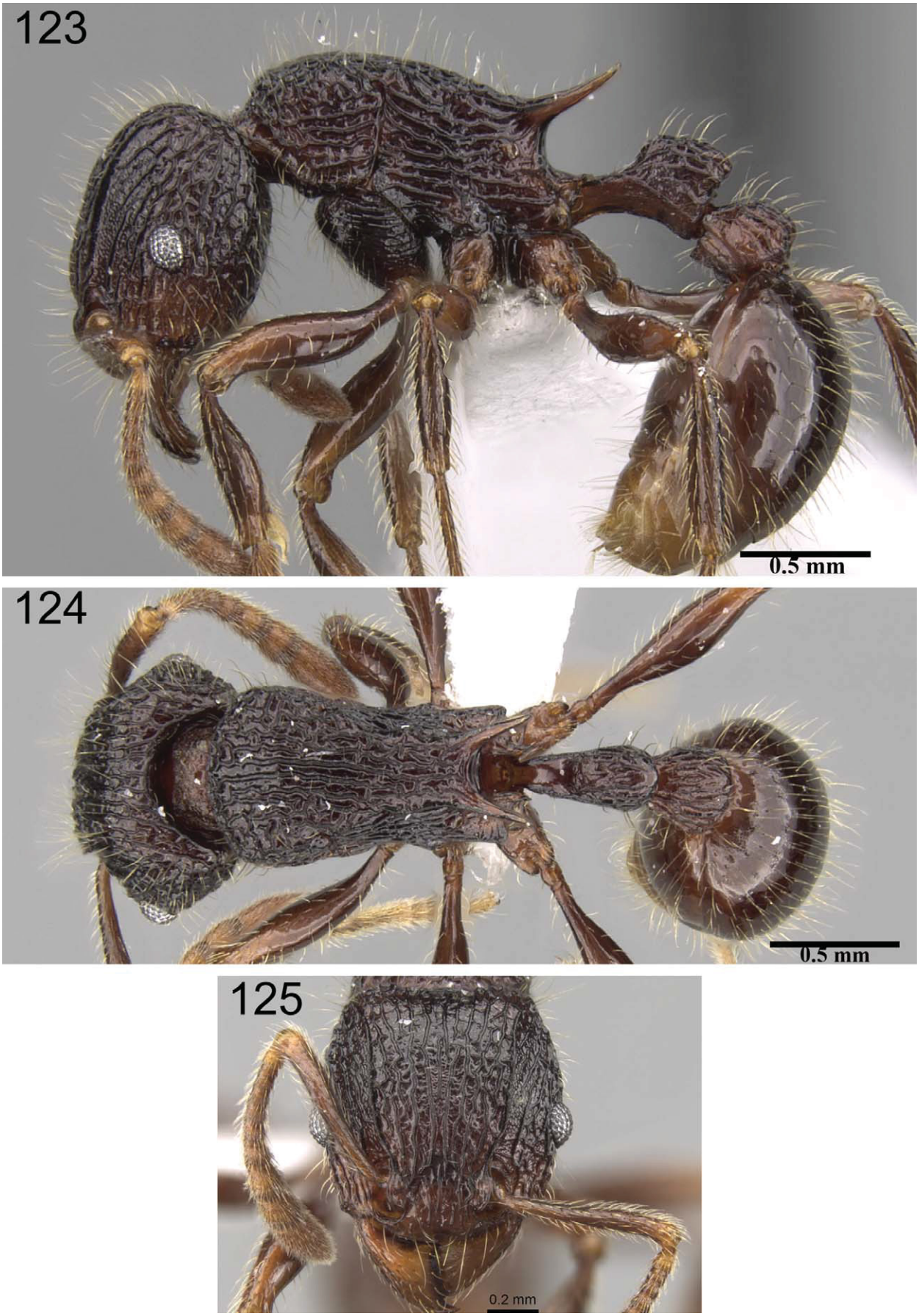
Within the *T. smaug* species complex, it is fairly easy to discriminate *T. adamsi* from the other species on the basis of the petiolar node shape. The node has the posterodorsal margin situated higher than the anterodorsal margin in *T. adamsi*, whereas both margins are at about the same height in the rest of the complex.

Etymology

The name of the new species is a patronym in honour of the British writer Douglas Adams (1952–2001), best known for “The Hitchhiker's Guide to the Galaxy” series.

Material examined

MADAGASCAR: Antsiranana, R.S. Manongarivo, 14.5 km 220° SW Antanambao, 13.99833 S, 48.42833 E, 1175 m, montane rainforest, 19.–25.X.1998 (*B.L. Fisher*); Mahajanga, Bemanevika, Souspref. de Bealanana, forest, 20. X. 1975 (*A. Peyrieras*); Antsiranana, R.S. Manongarivo 17.3 km 218° SW Antanambao, 14.02167 S, 48.41833 E, 1580 m, montane rainforest, 27.X.1998 (*B.L. Fisher*); Antsiranana, R.S. Manongarivo, 20.4 km 219° SW Antanambao, 14.04667 S, 48.40167 E, 1860 m, montane rainforest, 3.XI.1998 (*B.L. Fisher*); Mahajanga, Bemanevika, Soupref. de Bealanana, 20.X.1975 (*A. Peyrieras*).



FIGURES 123–125. *T. adamsi*, holotype (CASENT0247345). **123.** Body in profile. **124.** Body in dorsal view. **125.** Head in full-face view.

Tetramorium latreillei Forel, 1895
(Figs. 16, 23, 126, 127, 128, 142)

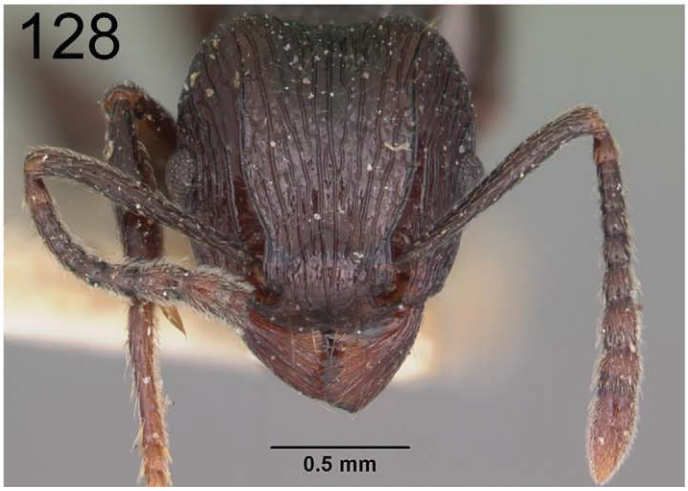
Tetramorium (*Xyphomyrmex*) *latreillei* Forel, 1895:247. Lectotype worker [designated here] MADAGASCAR, est Imerina ("eastern Imerina") (*Sikora*) (BMNH: CASENT0102340) [examined]. Paralectotypes, two workers with same data as lectotype (MHNG: CASENT0101291, CASENT0101292) [examined].
[Note: Bolton (1979) noted that all syntypes were located in the Forel collection in MHNG. However, we also found one syntype (the newly designated lectotype) in BMNH with the additional information "remounted B. Bolton 1975".]

Diagnosis
Tetramorium latreillei is clearly recognisable within the *T. smaug* complex because it is the only species without any standing hairs on the first gastral tergite.

Description
HL 1.05–1.06 (1.06); HW 1.06–1.08 (1.07); SL 0.82–0.85 (0.84); EL 0.23–0.24 (0.24); PH 0.52–0.55 (0.53); PW 0.72–0.76 (0.74); WL 1.37–1.40 (1.38); PSL 0.54–0.56 (0.55); PTL 0.34–0.35 (0.35); PTH 0.41–0.43 (0.42); PTW 0.27–0.30 (0.29); PPL 0.30–0.32 (0.31); PPH 0.43–0.45 (0.44); PPW 0.40–0.44 (0.42); CI 100–101 (101); SI 77–79 (79); OI 22 (22); DMI 53–55 (54); LMI 38–39 (39); PSLI 50–53 (52); PeNI 38–39 (39); LPeI 81–85 (83); DPeI 79–86 (83); PpNI 55–58 (56); LPpI 70–72 (71); DPpI 132–138 (134); PPI 141–148 (145) (three measured).

Head as long as wide to weakly wider than long (CI 100–101); posterior head margin strongly concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes well-developed, moderately deep, but narrow, and without defined posterior and ventral margins. Antennal scapes short, not reaching posterior head margin (SI 77–79). Eyes of moderate size (OI 22). Mesosomal outline in profile flat, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–39). Propodeal spines massively developed with very broad base, extremely long, and acute (PSLI 50–53); propodeal lobes short and rounded. Petiolar node in profile rectangular nodiform, around 1.2 times higher than long (LPeI 81–85), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum slightly convex; node in dorsal view between 1.1 to 1.3 times longer than wide (DPeI 79–86). Postpetiole in profile subglobular, weakly anteroposteriorly compressed, approximately 1.4 times higher than long (LPpI 70–72); in dorsal view around 1.3 to 1.4 times wider than long (DPpI 132–138). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view about 1.4 to 1.5 times wider than petiolar node (PPI 141–148). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose, with three to five rugae; cephalic dorsum between frontal carinae with 9 to 12 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted or with cross-meshes; lateral and ventral head longitudinally rugose, rarely with cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae with very distinct and pronounced longitudinal rugae. Waist segments longitudinally rugose, rugae on waist segments weaker than on head and mesosoma, especially dorsally. Gaster completely unsculptured, smooth, and shining. Ground sculpture generally faint to absent everywhere on body. Head with abundant standing hairs; mesosoma with up to two pairs restricted to pronotal dorsum; remainder of mesosoma, waist segments, and first gastral tergite without standing hairs; first gastral tergite with moderately dense appressed pubescence. Anterior edges of antennal scapes with appressed hairs. Body a uniform very dark brown to black colour.

Notes
Unfortunately, no modern material is available. The original type series is from "eastern Imerina" (Forel, 1895), which might be located in central-eastern Madagascar. The exact type locality remains unknown, making it difficult to resample new material. It is surprising, though, that no more specimens have been collected in the last 120 years, especially considering the large sampling effort undertaken by the Malagasy ant inventory project (Fisher, 2005).



FIGURES 126–128. *T. latreillei*, lectotype (CASENT0102340). **126.** Body in profile. **127.** Body in dorsal view. **128.** Head in full-face view.

Within the species complex, *T. latreillei* is the only species lacking standing hairs on the first gastral tergite, and is thus easily identifiable. Even without considering this character, it cannot be misidentified with *T. adamsi* due to the petiolar node of the latter, which has the posterodorsal margin higher than the anterodorsal margin. Shorter antennal scapes separate *T. latreillei* from *T. nazgul* (SI 89–93), and the very dark brown to black colouration distinguishes it from *T. marojejy*, which is of orange colour. However, *T. latreillei* is very close to *T. sabatra* and *T. smaug*. All three species share the same morphometric range, and superficially possess a similar overall habitus. They have massively constructed, extremely long propodeal spines, reduced hairiness, and very dark brown to black colouration. This character combination clearly separates these three species from the remainder of the complex. As noted above, *T. latreillei* can be easily separated from *T. sabatra* and *T. smaug* by the pilosity/pubescence on the first gastral tergite. The latter two have only very sparse, short pubescence and few to many long, standing hairs on the first gastral tergite, whereas *T. latreillei* does not have a single standing hair, but instead a moderately dense, appressed pubescence.

It is possible that all three species are conspecific, and that the differences in pilosity/pubescence represent geographical variation. The overall morphological similarity might support this hypothesis, as well as the fact that none of the three species was found in sympatry. However, our own studies (Hita Garcia et al., 2010; Hita Garcia & Fisher, 2011, 2012), as well as previous studies on *Tetramorium* (Bolton, 1976, 1977, 1979, 1980), concur that pilosity and pubescence patterns are generally very species-specific. The hairs on the mesosoma and first gastral tergite represent a particularly good diagnostic character. *Tetramorium latreillei*, *T. sabatra* and *T. smaug* all seem to be relatively rare, making them unlikely to be found in the same locality. The distribution ranges of the three, however, strongly overlap. We currently consider all three distinct species that can be well separated, although the species delimitations presented herein might change with additional material.

Material examined
MADAGASCAR: Imerina (*Sikora*).

***Tetramorium marojejy* Hita Garcia & Fisher sp. n.**
(Figs. 18, 21, 22, 129, 130, 131, 142)

Holotype worker, MADAGASCAR, Antsiranana, Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 14.44333 S, 49.74333 E, 1325 m, montane rainforest, canopy moss and leaf litter, collection code BLF09192, 19.XI.2003 (*B.L. Fisher*) (CASC: CASENT0247334). Paratypes, 8 workers with same data as holotype (CASC: CASENT0247327; CASENT0247328; CASENT0247329; CASENT0247330; CASENT0247333; CASENT0499782; CASENT0499783; CASENT0499784).

Diagnosis
Tetramorium marojejy can be easily distinguished from the remainder of the species complex by the following character combination: antennal scapes short to moderate (SI 79–85); propodeal spines long to very long (PSLI 34–37); anterodorsal and posterodorsal margins of petiolar node situated at about same height; first gastral tergite with numerous standing hairs; uniform orange to pale brown body colour.

Description
HL 1.07–1.14 (1.11); HW 1.00–1.07 (1.05); SL 0.82–0.88 (0.85); EL 0.23–0.25 (0.24); PH 0.50–0.59 (0.54); PW 0.72–0.78 (0.75); WL 1.36–1.49 (1.42); PSL 0.36–0.41 (0.40); PTL 0.35–0.37 (0.36); PTH 0.37–0.41 (0.39); PTW 0.27–0.31 (0.29); PPL 0.35–0.37 (0.36); PPH 0.37–0.41 (0.39); PPW 0.36–0.39 (0.37); CI 91–96 (94); SI 79–85 (81); OI 22–24 (23); DMI 52–54 (53); LMI 37–39 (38); PSLI 34–37 (36); PeNI 37–39 (39); LPeI 89–97 (93); DPeI 77–84 (80); PpNI 49–51 (50); LPpI 88–95 (91); DPpI 101–109 (105); PPI 125–135 (129) (12 measured).

Head longer than wide (CI 91–96); posterior head margin distinctly concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior

head margin. Antennal scrobes developed, but very shallow and narrow, without defined posterior and ventral margins. Antennal scapes of moderate length, not reaching posterior head margin (SI 79–85). Eyes of moderate size (OI 22–24). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–39). Propodeal spines long, spinose and acute (PSLI 34–37); propodeal lobes well-developed, triangular to elongate-triangular, and acute. Petiolar node in profile rectangular nodiform, approximately 1.0 to 1.1 times higher than long (LPeI 89–97), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height, dorsum flat to weakly convex; node in dorsal view approximately 1.2 to 1.3 times longer than wide (DPeI 77–84). Postpetiole in profile globular, approximately 1.1 times higher than long (LPpI 88–95); in dorsal view around 1.0 to 1.1 times wider than long (DPpI 101–109). Postpetiole in profile approximately as high as petiolar node and generally appearing slightly less voluminous, in dorsal view approximately 1.2 to 1.4 times wider than petiolar node (PPI 125–135). Mandibles striate; clypeus longitudinally rugose, with four to six rugae, median ruga always present and distinct, remaining rugae variably developed; cephalic dorsum between frontal carinae with 9 to 11 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted, rarely with cross-meshes; lateral and ventral head longitudinally rugose to reticulate-rugose. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae with well-developed and conspicuous longitudinal rugae. Waist segments strongly longitudinally rugose. Gaster unsculptured, smooth, and shining. Ground sculpture generally faint to absent everywhere on body. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with suberect to erect hairs. Body of uniform orange to pale brown colour.

Notes

Tetramorium marojejy is currently only known from two localities: the type locality Marojejy and Anjanaharibe-Sud. Both localities are montane rainforests located in north-eastern Madagascar at altitudes of 1200 to 1325 m. In addition, the new species was mainly collected from leaf litter.

Inside the *T. smaug* complex the orange to pale brownish *T. marojejy* is the only species without a dark brown to blackish body colouration, and thus is easily recognisable. However, not considering body colour, the species differs from *T. latreillei*, *T. sabatra*, and *T. smaug* in the development of the propodeal spines and pilosity. The latter three species all have massive and extremely long propodeal spines (PSLI 48–72) and have either no, few, or several scattered standing hairs on the first gastral tergite, whereas *T. marojejy* has much less extremely developed propodeal spines (PSLI 34–37) and numerous standing hairs on the first gastral tergite. *Tetramorium marojejy* also cannot be confused with *T. adamsi* since the latter species possesses a petiolar node with the posterodorsal margin situated higher than the anterodorsal while both margins are at about the same height in *T. marojejy*. The remaining species, *T. nazgul*, is dark brown to black in colour and therefore is also unlikely to be misidentified with the orange to pale brown *T. marojejy*. The latter has shorter antennal scapes (SI 79–85), a comparatively lower petiolar node (LPeI 89–97), and a lower and narrower postpetiole (LPpI 88–95; DPpI 101–109) than *T. nazgul* (SI 89–92; LPeI 81–88; LPpI 78–85; DPpI 113–122).

Etymology

This new species is named after the type locality, the Park National de Marojejy, which is one of the most important places for the conservation of biodiversity in Madagascar due to the extraordinarily high diversity of landscapes, habitats, fauna and flora. The species epithet is a noun in apposition, and thus invariant.

Material examined

MADAGASCAR: Antsiranana, 9.2 km WSW Befingotra, Rés. Anjanaharibe-Sud, 14.75 S, 49.46667 E, 1200–1260 m, montane rainforest, 9.–11.XI.1994 (*B.L. Fisher*); Antsiranana, Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 14.44333 S, 49.74333 E, 1325 m, montane rainforest, 19.XI.2003 (*B.L. Fisher*).

FIGURES 129–131. *T. marojejy*, holotype (CASENT0247334). **129.** Body in profile. **130.** Body in dorsal view. **131.** Head in full-face view.

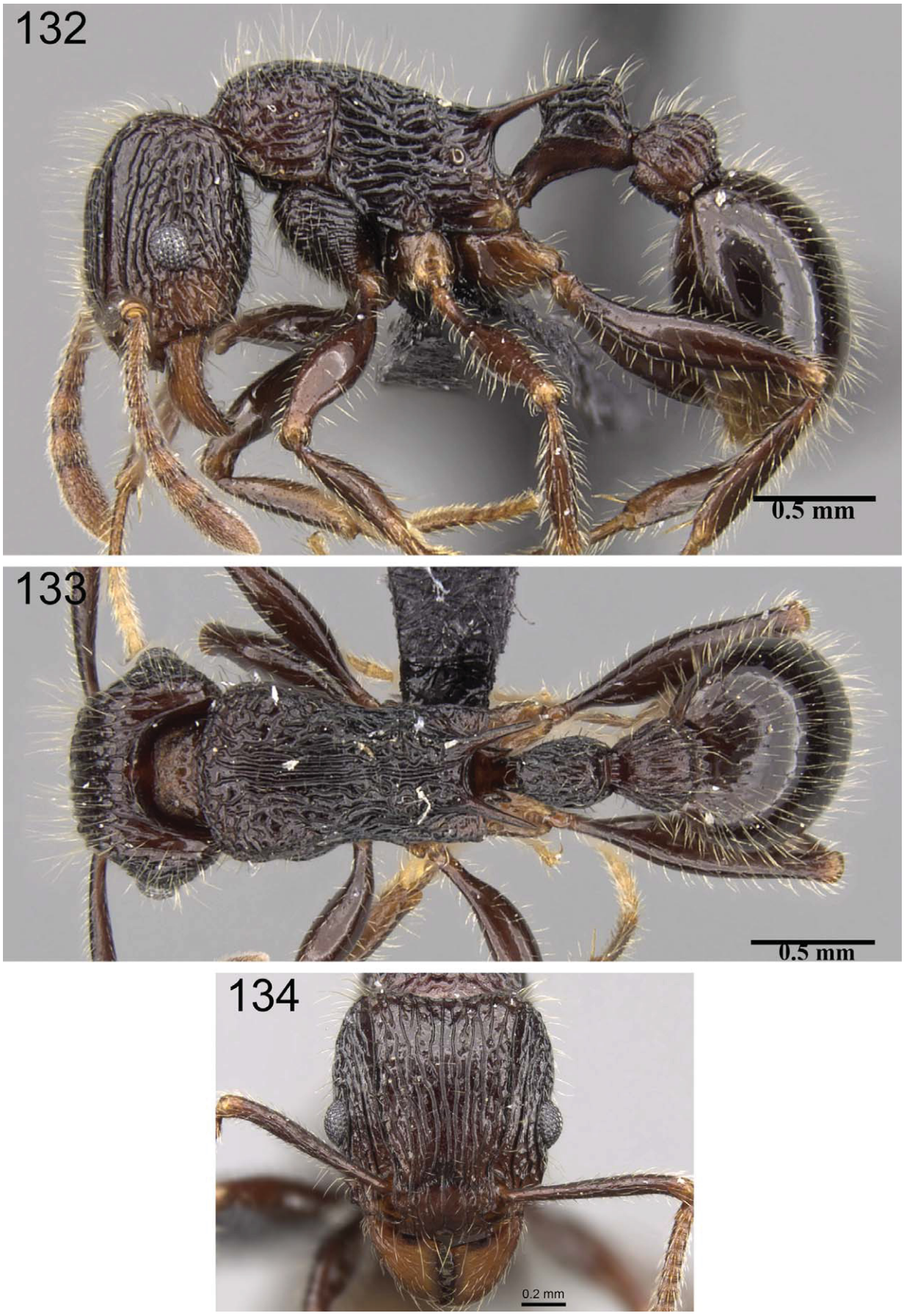
***Tetramorium nazgul* Hita Garcia & Fisher sp. n.**
(Figs. 19, 20, 132, 133, 134, 142)

Holotype worker, MADAGASCAR, Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18.26667 S, 45.40667 E, 1050 m, montane rainforest, sifted litter (leaf mold, rotten wood), collection code BLF07020, 13.–17.I.2003 (*B.L. Fisher, C. Griswold et al.*) (CASENT: CASENT0028625). Paratypes, 31 workers with same data as holotype (BMNH: CASENT0028584; CASC: CASENT0028579; CASENT0028585; CASENT0028590; CASENT0028591; CASENT0028601; CASENT0028604; CASENT0028605; CASENT0028606; CASENT0028610; CASENT0028620; CASENT0028621; CASENT0028622; CASENT0028626; CASENT0028627; CASENT0028628; CASENT0028632; CASENT0028636; CASENT0028652; CASENT0028663; CASENT0028670; CASENT0028671; CASENT0028674; CASENT0028678; CASENT0028680; CASENT0028681; CASENT0028689; CASENT0028690; MCZ: CASENT0028595; MHNG: CASENT0028594; NHMB: CASENT0028592).

Diagnosis
The following character combination renders *T. nazgul* easily diagnosable within the *T. smaug* species complex: antennal scapes comparatively long (SI 89–92); propodeal spines very long (PSLI 39–43); anterodorsal and posterodorsal margins of petiolar node situated at about same height; first gastral tergite with numerous standing hairs; dark brown to black body colour.

Description
HL 0.95–1.06 (1.02); HW 0.85–0.98 (0.93); SL 0.79–0.89 (0.84); EL 0.21–0.24 (0.22); PH 0.48–0.56 (0.53); PW 0.67–0.75 (0.73); WL 1.23–1.39 (1.34); PSL 0.38–0.45 (0.42); PTL 0.31–0.36 (0.34); PTH 0.38–0.43 (0.41); PTW 0.26–0.31 (0.29); PPL 0.31–0.36 (0.33); PPH 0.38–0.42 (0.41); PPW 0.35–0.41 (0.39); CI 90–92 (91); SI 89–92 (90); OI 23–25 (24); DMI 54–57 (55); LMI 37–41 (39); PSLI 39–43 (41); PeNI 37–42 (40); LPeI 81–88 (84); DPeI 82–89 (86); PpNI 51–55 (54); LPpI 78–85 (81); DPpI 113–122 (118); PPI 127–140 (133) (12 measured).

Head distinctly longer than wide (CI 90–92); posterior head margin concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes developed, shallow and narrow, without defined ventral margins. Antennal scapes of moderate length, not reaching posterior head margin (SI 89–92). Eyes of moderate size (OI 23–25). Mesosomal outline in profile flat to weakly convex, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–41). Propodeal spines very long, spinose and acute (PSLI 39–43); propodeal lobes well-developed, triangular, and usually acute. Petiolar node in profile rectangular nodiform, approximately 1.1 to 1.2 times higher than long (LPeI 81–88), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height, dorsum flat to weakly convex; node in dorsal view approximately 1.1 to 1.2 times longer than wide (DPeI 82–89). Postpetiole in profile globular, approximately 1.2 to 1.3 times higher than long (LPpI 78–85); in dorsal view around 1.1 to 1.2 times wider than long (DPpI 113–122). Postpetiole in profile appearing approximately as voluminous as petiolar node, in dorsal view approximately 1.3 to 1.4 times wider than petiolar node (PPI 127–140). Mandibles striate; clypeus longitudinally rugose/rugulose, with three to eight rugae/rugulae, median ruga usually present and distinct, remaining rugae/rugulae variably developed, usually weaker than median ruga; cephalic dorsum between frontal carinae with 8 to 13 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted and with cross-meshes; scrobal area mostly unsculptured; lateral and ventral head longitudinally rugose to reticulate-rugose. Mesosoma laterally and dorsally mainly longitudinally rugose. Forecoxae with well-developed and conspicuous longitudinal rugae. Waist segments strongly rugose. Gaster unsculptured, smooth, and shining. Ground sculpture generally faint to absent everywhere on body. All dorsal surfaces of head, mesosoma, waist segments, and gaster with abundant, long, and fine standing hairs. Anterior edges of antennal scapes with suberect to erect hairs. Body of uniform dark brown to black colour, often appendages of slightly lighter colour.



FIGURES 132–134. *T. nazgul*, holotype (CASENT0028625). **132.** Body in profile. **133.** Body in dorsal view. **134.** Head in full-face view.

Notes

This new species is known from few specimens from Analalava and Zombitse, both tropical dry forests, and a high number of specimens from the type locality Ambohijanahary, which is a montane rainforest. The altitudinal range is 700 to 1100 m, and *T. nazgul* appears to be a leaf litter inhabitant.

Within the *T. smaug* species complex, it is easily separated from the three species *T. latreillei*, *T. sabatra*, and *T. smaug* which have extremely long and massively developed propodeal spines with a very broad base (PSLI 48–72), whereas the spines of *T. nazgul* are very long, but less massive and without such a broad base (PSLI 39–43). *Tetramorium adamsi*, which is only known from the area around Manongarivo, has a petiolar node shape with the posterodorsal margin situated higher than the anterodorsal, whereas in *T. nazgul* both margins are about the same height. The last species of the complex, *T. marojejy*, is also very unlikely to be confused with *T. nazgul*. The most obvious character is colouration (orange to light brown in *T. marojejy* versus dark brown to black in *T. nazgul*), but they also differ in antennal scape length and shape of the waist segments. *Tetramorium nazgul* has longer antennal scapes (SI 89–92), a relatively longer petiolar node (LPeI 81–88), and a higher and broader postpetiole (LPpI 78–85; DPpI 113–122) than *T. marojejy* (SI 79–85; LPeI 89–97; LPpI 88–95; DPpI 101–109).

Etymology

The species name "*nazgul*" is taken from J.R.R. Tolkien's "The Lord of the Rings" and refers to the evil ring-wraiths who serve the main villain "Sauron". The species epithet is an arbitrary combination of letters.

Material examined

MADAGASCAR: Fianarantsoa, Forêt d'Analalava, 29.6 km 280° W Ranohira, 22.59167 S, 45.12833 E, 700 m, tropical dry forest, 1.–5.II.2003 (*B.L. Fisher, C. Griswold et al.*); Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18.26667 S, 45.40667 E, 1050 m, montane rainforest, 13.–17.I.2003 (*B.L. Fisher, C. Griswold et al.*); Toliara, Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 34.6 km 314° NW Ambaravaranala, 18.26 S, 45.4183 E, 1100 m, montane rainforest, 16.I.2003 (*B.L. Fisher, C. Griswold et al.*); Toliara, Parc National de Zombitse, 19.8 km 84° E Sakaraha, 22.84333 S, 44.71 E, 770 m, tropical dry forest, 5.–9.II.2003 (*B.L. Fisher, C. Griswold et al.*).

***Tetramorium sabatra* Hita Garcia & Fisher sp. n.**

(Figs. 11, 15, 24, 25, 26, 135, 136, 137, 142)

Holotype worker, MADAGASCAR, Toliara, Rés. Andohahela, 11 km NW Enakara, 24.56667 S, 46.83333 E, 800 m, montane rainforest, pitfall trap, collection code BLF00490, 16.XI.1992 (*B.L. Fisher*) (CASC: CASENT0189241). Paratypes, three workers with same data as holotype (CASC: CASENT0218056; CASENT0218057; CASENT0270780); one worker from Toliara, Rés. Andohahela, 11 km NW Enakara, 24.56667 S, 46.83333 E, 800 m, montane rainforest, from sifted litter, collection code BLF00492, 17.XI.1992 (*B.L. Fisher*) (CASC: CASENT0189240); and one worker from Toliara, Rés. Andohahela, 10 km NW Enakara, 24.56667 S, 46.81667 E, 430 m, rainforest, sifted litter, collection code BLF00522, 22.XI.1992 (*B.L. Fisher*) (CASC: CASENT0189239).

Diagnosis

Tetramorium sabatra is easily distinguished from the other group members by the following character combination: antennal scapes comparatively short (SI 73–80); extremely long and massively constructed propodeal spines (PSLI 48–72); anterodorsal and posterodorsal margins of petiolar node situated at about same height; mesosoma with one or two pairs of standing hairs, restricted to dorsal pronotum; hairs on leading edge of antennal scapes usually strongly appressed; first gastral tergite with few standing hairs and very sparse, short pubescence; very dark brown to black colouration.

Description

HL 1.00–1.12 (1.04); HW 1.02–1.13 (1.05); SL 0.76–0.90 (0.82); EL 0.20–0.23 (0.21); PH 0.48–0.54 (0.50); PW 0.71–0.79 (0.75); WL 1.27–1.41 (1.33); PSL 0.50–0.81 (0.60); PTL 0.34–0.37 (0.36); PTH 0.39–0.44 (0.41); PTW 0.27–0.31 (0.28); PPL 0.30–0.34 (0.32); PPH 0.40–0.46 (0.42); PPW 0.37–0.44 (0.39); CI 100–103 (101); SI 73–80

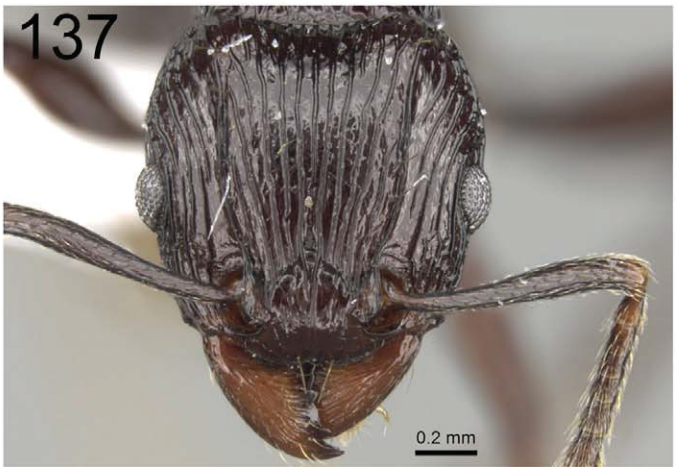
(77); OI 18–21 (20); DMI 55–58 (56); LMI 37–40 (38); PSLI 48–72 (57); PeNI 36–39 (38); LPeI 82–90 (87); DPeI 75–86 (80); PpNI 50–56 (52); LPpI 71–77 (75); DPpI 119–129 (125); PPI 134–143 (138) (ten measured).

Head as long as wide to weakly wider than long (CI 100–103); posterior head margin strongly concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes well-developed, moderately deep, but narrow, and without defined posterior and ventral margins. Antennal scapes short to moderate, not reaching posterior head margin (SI 73–80). Eyes small to moderate (OI 18–21). Mesosomal outline in profile flat, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 37–40). Propodeal spines massively developed with very broad base, extremely long, and acute (PSLI 48–72); propodeal lobes short and blunt. Petiolar node in profile rectangular nodiform, approximately 1.1 to 1.2 times higher than long (LPeI 82–90), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum slightly convex; node in dorsal view approximately 1.1 to 1.3 times longer than wide (DPeI 75–86). Postpetiole in profile subglobular, weakly anteroposteriorly compressed, approximately 1.3 to 1.4 times higher than long (LPpI 71–77); in dorsal view around 1.2 to 1.3 times wider than long (DPpI 119–129). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view approximately 1.3 to 1.5 times wider than petiolar node (PPI 134–143). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose, with three to five rugae; cephalic dorsum between frontal carinae with 9 to 12 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted or with cross-meshes; lateral and ventral head longitudinally rugose, rarely with cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae with very distinct and pronounced longitudinal rugae. Waist segments longitudinally rugose, rugae on waist segments weaker than on head and mesosoma, especially dorsally. Gaster completely unsculptured, smooth, and shining. Ground sculpture generally faint to absent everywhere on body. Head with abundant standing hairs; hairs on mesosoma restricted to dorsal pronotum, usually one or two pairs of hairs present, rarely three pairs; waist segments and first gastral tergite with few to numerous standing hairs; first gastral tergite with very sparse, short, and appressed pubescence. Anterior edges of antennal scapes usually with appressed hairs (decumbent in one specimen). Body a uniform very dark brown to black colour.

Notes

Despite the comparatively small number of known specimens (15 in total), *T. sabatra* seems to be widely distributed in the rainforests and montane rainforests of eastern Madagascar, as well as in Analavelona in the southwest. The southernmost locality is the type locality, Andohahela, and the northernmost locality is Montagne d'Akirindro. In-between it is only known from few more localities. Furthermore, *T. sabatra* seems to inhabit forests at elevations of 430 to 1300 m, and was mainly collected from the ground. The scarcity of material and wide distribution range suggests that this species is fairly rare, uncommon, or just sampled inappropriately. Four out of the fifteen specimens were collected while visiting the flowers of *Impatiens mandrakae* Fischer & Rahelivololona (Balsaminaceae) at Mandraka. This suggests that *T. sabatra* lives in the vegetation and is therefore rarely sampled from the ground. This could be true for *T. latreillei* and *T. smaug*, too, and might explain the rarity of these three species.

Inside the *T. smaug* complex, *T. sabatra* is unlikely to be misidentified with *T. adamsi*, *T. marojejy*, and *T. nazgul*. The latter three have numerous standing hairs on the first gastral tergite, and are much hairier than *T. sabatra*. Furthermore, *T. adamsi* has a petiolar node shape with the posterodorsal margin situated higher than the anterodorsal, while both margins are at the same height in *T. sabatra*. *Tetramorium nazgul* also has much longer antennal scapes (SI 89–93), and *T. marojejy* is of orange to light brown body colour. Nevertheless, *T. sabatra* appears to be morphologically most closely associated with *T. latreillei* and *T. smaug* since they share the same morphometric range and have a very similar gestalt. They are very darkly coloured species with massively developed propodeal spines and reduced hairiness. However, *T. sabatra* can be well separated from *T. latreillei* due to the absence of standing hairs on the first gastral tergite in the latter, whereas a few to several standing hairs are always present in *T. sabatra*. In addition, the latter species has only very sparse and inconspicuous pubescence on the first gastral tergite while *T. latreillei* has moderately dense and distinct pubescence. *Tetramorium smaug* mainly differs from *T. sabatra* in the number of hairs on the mesosomal dorsum. The latter has just one or two pairs on the pronotal dorsum, whereas *T. smaug* has 7 to 14 pairs throughout the whole mesosomal dorsum. Also, in *T. sabatra* the hairs on the leading edges of the antennal scapes are usually appressed but subdecumbent to suberect in *T. smaug*.



FIGURES 135–137. *T. sabatra*, holotype (CASENT0189241). **135.** Body in profile. **136.** Body in dorsal view. **137.** Head in full-face view.

As noted in the above descriptions, *T. latreillei*, *T. sabatra*, and *T. smaug* could all belong to one species with considerable variation in patterns of pilosity/pubescence. However, as previously discussed, we are of the opinion that these characters are generally of high diagnostic value at the species level, which leads us to treat the three as distinct species. The available material is limited, however, and more material could demonstrate that our current species delimitations are incorrect.

Etymology
The species epithet is an arbitrary combination of letters.

Material examined
MADAGASCAR: Antananarivo, Mandraka, 18° 54' 46" S, 47° 53' 32" E, ca. 1200 m, 23.I.2006 (*A. Erpenbach*); Fianarantsoa, Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, 23.83517 S, 46.96367 E, 940 m, 15.XI.2006 (*B.L. Fisher et al.*); Toamasina, F.C. Didy, 18.19833 S, 48.57833 E, 960 m, 16.–23.XII.1998 (*H.J. Ratsirarson*); Toamasina, Montagne d'Akirindro, 7.6 km 341° NNW Ambinanitelo, 15.28833 S, 49.54833 E, 600 m, rainforest, 17.–21.III.2003 (*B.L. Fisher, C. Griswold et al.*); Toliara, Forêt Classée d'Analavelona, 33.2 km 344° NNW Mahaboboka, 22.64333 S, 44.17167 E, 1300 m, 22.–26.II.2003 (*B.L. Fisher, C. Griswold et al.*); Toliara, Rés. Andohahela, 11 km NW Enakara, 24.56667 S, 46.83333 E, 800 m, montane rainforest, 16.–17.XI.1992 (*B.L. Fisher*); Toliara, Rés. Andohahela, 10 km NW Enakara, 24.56667 S, 46.81667 E, 430 m, rainforest, 22.XI.1992 (*B.L. Fisher*).

Tetramorium smaug Hita Garcia & Fisher sp. n.
(Figs. 27, 28, 138, 139, 140, 142)

Holotype worker, MADAGASCAR, Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.83937 S, 48.30842 E, 1080 m, montane rainforest, pitfall trap, collection code BLF16917, 4.–7.V.2007 (*B.L. Fisher et al.*) (CASC: CASENT0121244). Paratype, one worker with same data as holotype (CASC: CASENT0124788).

Diagnosis
Tetramorium smaug can be easily discriminated from the remainder of the species complex by the following character set: antennal scapes comparatively short (SI 77–81); extremely long and massively constructed propodeal spines (PSLI 57–63); anterodorsal and posterodorsal margins of petiolar node situated at about same height; mesosoma with 7 to 14 pairs of standing hairs; hairs on leading edge of antennal scapes subdecumbent to suberect; first gastral tergite with several scattered standing hairs and very sparse, short, appressed pubescence; very dark brown to black colouration.

Description
HL 0.99–1.04 (1.02); HW 0.99–1.06 (1.02); SL 0.80–0.85 (0.81); EL 0.19–0.23 (0.21); PH 0.50–0.54 (0. 52); PW 0.70–0.77 (0.74); WL 1.30–1.38 (1.34); PSL 0.57–0.66 (0.60); PTL 0.30–0.38 (0.34); PTH 0.36–0.43 (0.40); PTW 0.25–0.32 (0. 29); PPL 0.30–0.32 (0.31); PPH 0.38–0.42 (0.41); PPW 0.36–0.41 (0.38); CI 100–102 (101); SI 77–81 (79); OI 19–22 (20); DMI 54–58 (56); LMI 38–40 (39); PSLI 57–63 (59); PeNI 35–41 (38); LPeI 77–91 (86); DPeI 79–88 (83); PpNI 48–55 (52); LPpI 73–79 (76); DPpI 120–132 (125); PPI 128–144 (135) (six measured).

Head as long as wide to weakly wider than long (CI 100–102); posterior head margin strongly concave. Anterior clypeal margin medially impressed. Frontal carinae strongly developed, diverging posteriorly, and ending at corners of posterior head margin. Antennal scrobes well-developed, moderately deep, but narrow and without defined posterior and ventral margins. Antennal scapes of moderate length, not reaching posterior head margin (SI 77–81). Eyes small to moderate (OI 19–22). Mesosomal outline in profile flat, moderately marginate from lateral to dorsal mesosoma; promesonotal suture and metanotal groove absent; mesosoma comparatively stout and high (LMI 38–40). Propodeal spines massively constructed with very broad base, extremely long, and acute (PSLI 57–63); propodeal lobes short and rounded. Petiolar node in profile rectangular nodiform, approximately 1.1 to 1.3 times higher than long (LPeI 77–91), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins approximately at same height, dorsum slightly convex; node in dorsal view approximately 1.1 to 1.3 times longer than wide (DPeI 79–88). Postpetiole in profile subglobular, weakly anteroposteriorly

compressed, approximately 1.2 to 1.4 times higher than long (LPpI 73–79); in dorsal view around 1.2 to 1.3 times wider than long (DPpI 120–132). Postpetiole in profile appearing less voluminous than petiolar node, in dorsal view approximately 1.3 to 1.5 times wider than petiolar node (PPI 128–144). Mandibles distinctly longitudinally rugose; clypeus longitudinally rugose, with three to five rugae; cephalic dorsum between frontal carinae with 9 to 12 longitudinal rugae, most rugae running unbroken from posterior head margin to anterior clypeus, few rugae interrupted or with cross-meshes; lateral and ventral head longitudinally rugose, rarely with cross-meshes. Mesosoma laterally and dorsally distinctly longitudinally rugose. Forecoxae with very distinct and pronounced longitudinal rugae. Waist segments longitudinally rugose, rugae on waist segments weaker than on head and mesosoma, especially dorsally. Gaster completely unsculptured, smooth, and shining. Ground sculpture generally faint to absent everywhere on body. Head with abundant standing hairs; mesosoma with 7 to 14 pairs of hairs; waist segments and first gastral tergite with few to several scattered, standing hairs; first gastral tergite with very sparse, short, and appressed pubescence. Anterior edges of antennal scapes with subdecumbent to suberect hairs. Body a uniform very dark brown to black colour.

Notes

The new species is currently only known from Ambatovy, Montagne d'Ambre, and Ivohibe. All three localities are montane rainforests at altitudes of 900 to 1300 m. However, these sites are geographically widely separated, one being located in the southeast, one in the east, and one in the northernmost tip of the island. This represents a fairly disjunctive distribution. Furthermore, the species is only known from six specimens, which could mean that it is very rare and uncommon, as seems to be the case with *T. latreillei* and *T. sabatra*. The scant available material was collected from pitfall traps, hand collecting, or rotten logs, which suggests that *T. smaug* is rarely encountered on the ground. As already stated in the description of *T. sabatra*, *T. smaug* might live in the vegetation, which could explain why it was only seldom sampled.

Within the *T. smaug* species complex, *T. smau*g cannot be mistaken for *T. adamsi* since the latter has a petiolar node with the posterodorsal margin situated higher than the anterodorsal margin. Also, it is unlikely to be confused with *T. nazgul* or *T. marojejy* because they are both much hairier than *T. smaug*. In addition, *T. nazgul* possesses the longest antennal scapes of the complex (SI 89–93) while the scapes of *T. smaug* are much shorter (SI 77–81). Moreover, *T. marojejy* differs also in body colour, which is orange to pale brown, whereas the body colour of *T. smaug* is very dark brown to black.

Tetramorium smaug is morphologically most closely associated with *T. latreillei* and *T. sabatra*. As mentioned above, the three species share the character combination of massive, extremely long propodeal spines, reduced hairiness, and very dark brown to back colouration. This character combination makes them unlikely to be confused with another species of the complex. *Tetramorium smaug* is also easily distinguished from *T. latreillei* and *T. sabatra*. *Tetramorium latreillei* has no standing hairs on the waist segments or the first gastral tergite, and displays moderately dense appressed pubescence on the first gastral tergite. This separates it clearly form *T. sabatra* and *T. smaug*. The latter two can also be easily distinguished from each other. *Tetramorium smaug* has 7 to 14 pairs of hairs throughout the mesosomal dorsum, whereas only one or two pairs are present in *T. sabatra*, and these are restricted to the pronotal dorsum. In addition, the hairs on the leading edge of the antennal scapes are generally strongly appressed in *T. sabatra* while they are subdecumbent to suberect in *T. smaug*.

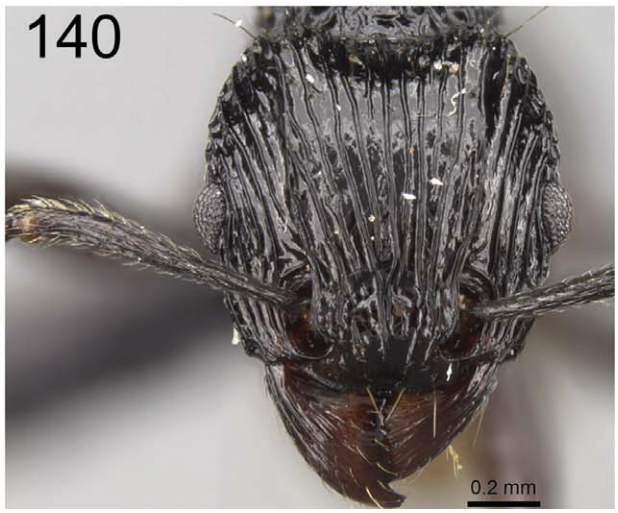
As discussed in the descriptions of *T. latreillei* and *T. sabatra*, there is a possibility that *T. smaug* is conspecific with one or even both of them. The lack of material in all three species makes species delimitations difficult, although we think that the differences in pilosity/pubescence are sufficient on the basis of the material examined in this study. At present, we treat all three as distinct species until more material becomes available.

Etymology

The new species was named after “Smaug”, the villain dragon from the fantasy novel “The Hobbit” written by J.R.R. Tolkien. The species epithet is an arbitrary combination of letters.

Material examined

MADAGASCAR: Antsiranana, Parc National Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 12.59639 S, 49.1595 E, 1300 m, montane rainforest, 2.–7.II.2001 (*B.L. Fisher, C. Griswold et al.*); Fianarantsoa, R.S. Ivohibe, 7.5 km ENE Ivohibe, 22.47 S, 46.96 E, 900 m, montane rainforest, 7.–12.X.1997 (*B.L. Fisher*); Toamasina, Ambatovy, 12.4 km NE Moramanga, 18.83937 S, 48.30842 E, 1080 m, montane rainforest, 4.–7.V.2007 (*B.L. Fisher et al.*).



FIGURES 138–140. *T. smaug*, holotype (CASENT0121244). **138.** Body in profile. **139.** Body in dorsal view. **140.** Head in full-face view.

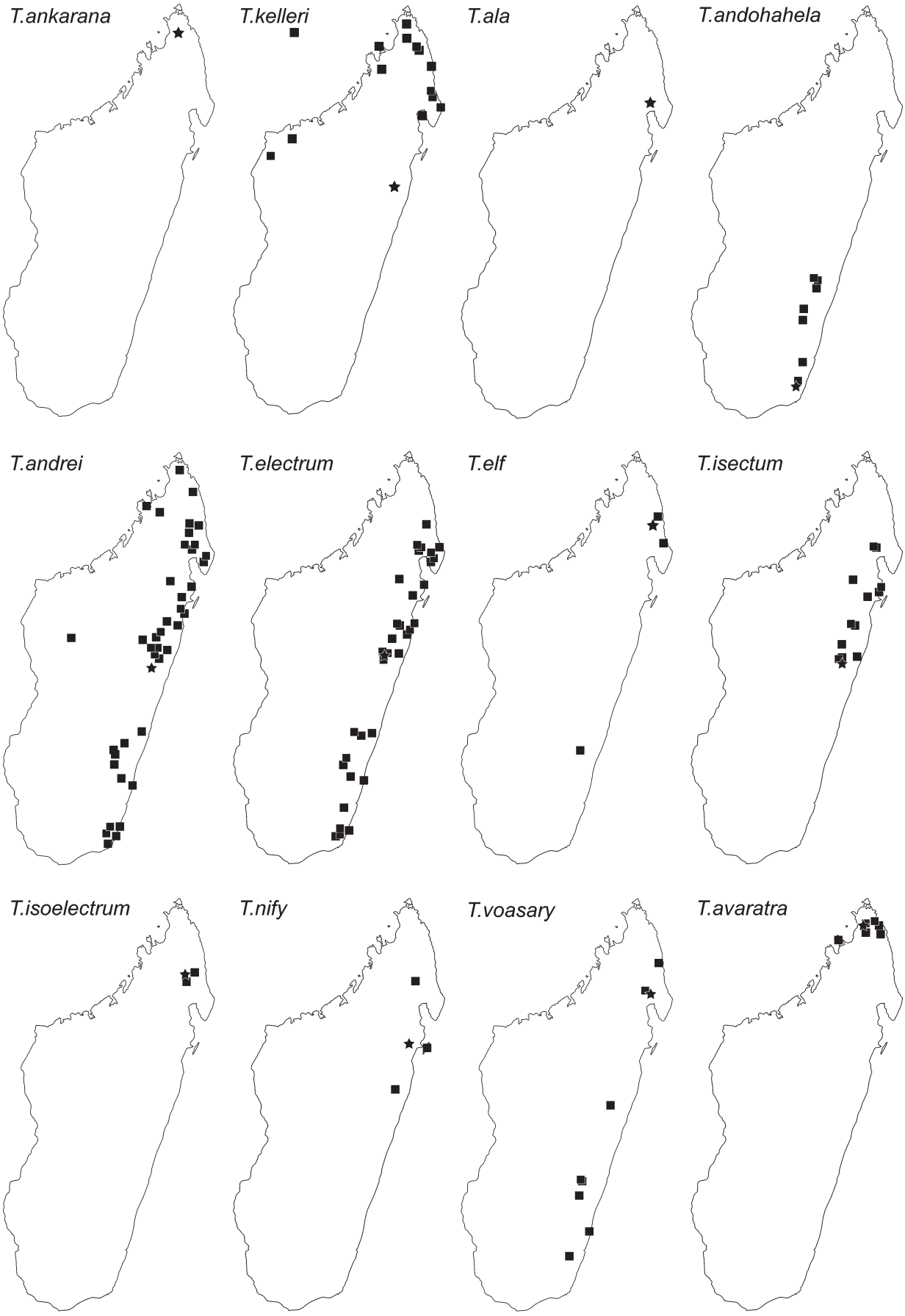


FIGURE 141. Geographic distribution maps of *Tetramorium* species treated in this study I. Star symbols represent type localities while rectangles represent all non-type localities.

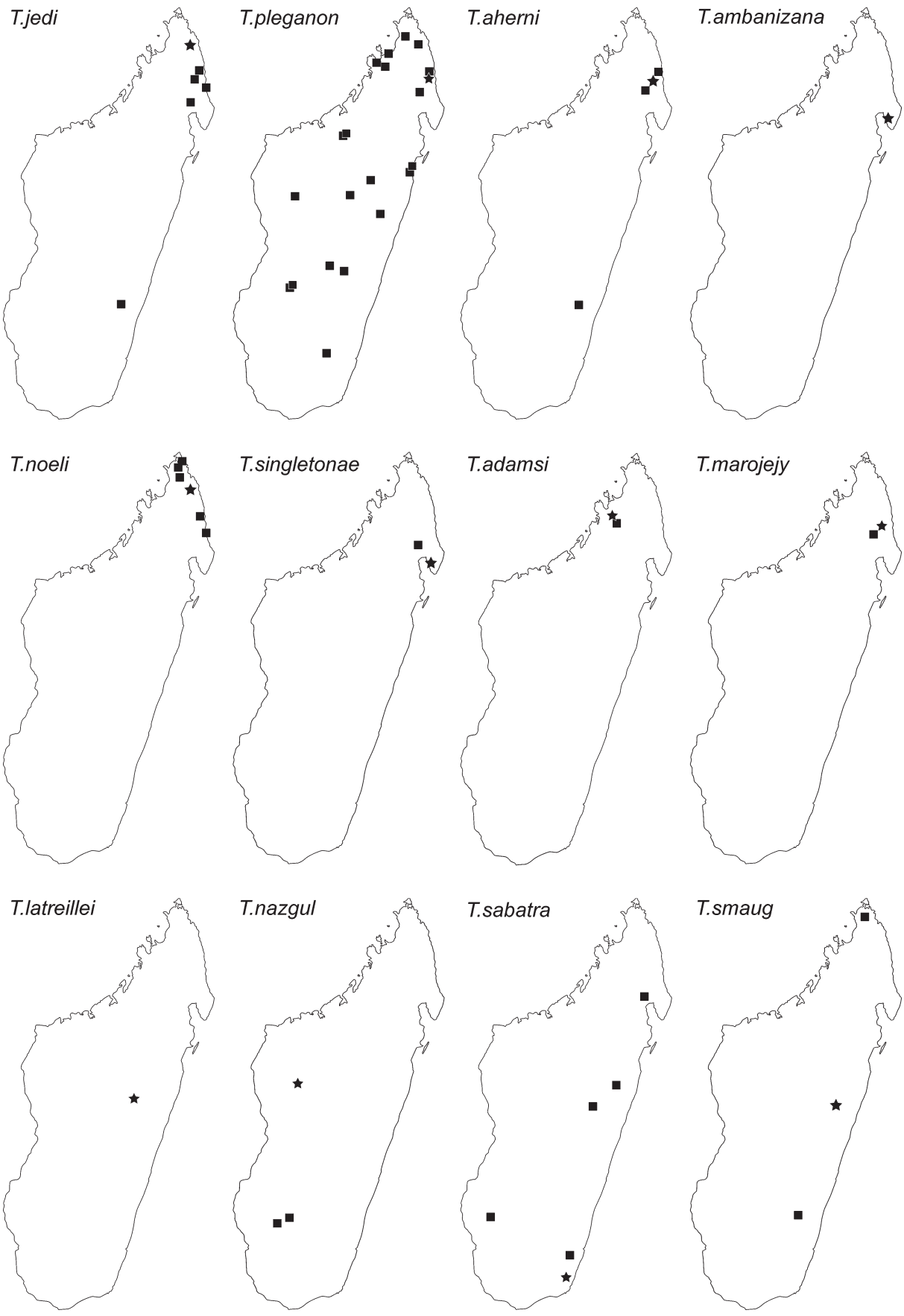


FIGURE 142. Geographic distribution maps of *Tetramorium* species treated in this study II. Star symbols represent type localities while rectangles represent all non-type localities. [Note: the type locality shown in the map for *T. latreillei* is only an approximation (see species re-description above for further information)].

Acknowledgements

First, we would like to thank Michele Esposito, from CASC, for her enduring support with databasing, image processing, proofreading, and her overall support in the lab. Then we are very thankful to our current and past imagers April Nobile, Erin Prado, Estella Ortega, and Shannon Hartman, all from CASC. Also, we appreciate the support from Ms. Suzanne Ryder, Ms. Natalie Dale-Skye Papilloud, and Dr. Gavin Broad from BMNH, Dr. Stefan Cover and Dr. Gary Alpert from MCZ, Dr. Daniel Burckhardt and Isabell Zürcher-Pfänder from NHMB, and Dr. Bernhard Merz from MHNG, who either loaned important type material or welcomed us to their collections. We also want to thank Prof. Phil S. Ward from the University of California, Davis, U.S.A., and Arne Erpenbach of Frankfurt, Germany, for providing material they collected in Madagascar. In addition, we would like to express our gratitude to John Longino, Barry Bolton, and an anonymous reviewer for editing and reviewing the manuscript. Moreover, the fieldwork on which this study is based could not have been completed without the gracious support of the Malagasy people and the Arthropod Inventory Team (Balsama Rajemison, Jean-Claude Rakotonirina, Jean-Jacques Rafanomezantsoa, Chrislain Ranaivo, Hanitriniana Rasoazanamavo, Nicole Rasoamanana, Clavier Randrianandrasana, Dimby Raharinjanahary, and Michael Bollinger). This study was supported by the National Science Foundation under Grant No. DEB-0072713, DEB-0344731, and DEB-0842395.

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